Columba Loquens: Pattern Recognition, Navigational Robustness and the Limits of Explanation in Avian Intelligence.

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Abstract

Keywords: homing pigeons; homing behaviour; classification; navigational cues; explanatory pluralism; underdetermination; robustness; system pressure; multisensory integration; model assessability.

This dissertation examines the extent to which homing pigeons can make consistent and reliable behavioural decisions under structural uncertainty, and which assumptions about internal processing prove necessary to understand these performances. The central question is whether performance sustainability leads to explanatory reduction, or whether multiple explanatory models remain empirically compatible with the same behavioural data. The research combines controlled experiments on pattern recognition and classification with field-based homing studies involving systematic variation of navigational cues. In the classification domain, behaviour is examined under variation in stimulus exemplars, including degradation and conflicting information. The results show proportional shifts in performance without an abrupt collapse of response structures. The data constrain strictly exemplar-specific binding, but do not compel reduction to a single necessary representational framework.

With regard to homing, the contribution of individual navigational cues is examined first. Manipulation of magnetic, olfactory, solar and visual sources of information produces measurable but gradual shifts in return rates and return times. Within the range investigated, no single cue proves strictly necessary or exclusively determinative. Cumulative variation of multiple cues is then applied. Although performance degradation occurs, no all-or-nothing transition or system collapse is observed within the parameter ranges employed. On the basis of these empirical findings, the assessability of explanatory models is analysed. Making assumptions concerning necessity, dominance and hierarchical ordering explicit reveals that strong exclusivity claims are not descriptively unavoidable. At the same time, systematic variation does not eliminate alternative explanatory frameworks. Explanatory pluralism therefore proves not to be merely a temporary consequence of data limitations, but a persistent feature within the range investigated.

The central conclusion is that robust maintenance of behavioural performance does not coincide with explanatory reduction. Homing pigeons display consistent decision-making under controlled uncertainty, while multiple structures of assumptions remain empirically compatible with the same behavioural outcomes. In this domain, stability and underdetermination prove to be simultaneously occurring properties of the same behavioural system. The findings are strictly limited to the experimental design and range of variation employed, but contribute to a more precise delineation of the relationship between functioning and explanation in scientific research on complex behaviour.

Management Summary of the dissertation 'Columba Loquens: Pattern Recognition, Navigational Robustness and the Limits of Explanation in Avian Intelligence'

Chapter 1 (Introduction: Reliable Performance, Inadequate Explanations and the Need for Repositioning)

Chapter 1 positions the central problem of this dissertation: the tension between reliable behavioural performance and inadequate explanations of that performance. Within the natural sciences, systems may function consistently while the underlying explanations are only partially and satisfactorily articulated. In this dissertation, 'explanation' is understood not as a complete mechanistic reconstruction, but as a coherent set of assumptions that renders behaviour plausible and reproducible. The specific research domain concerns homing pigeons (Columba livia) as a biological model. These organisms display stable performance in pattern recognition and homing, including under variable or incomplete information conditions. This robustness makes the domain epistemologically relevant: performance remains consistent while multiple explanatory models are simultaneously compatible with the observed outcomes. Explanatory pluralism is therefore treated not as a temporary lacuna, but as a potentially structural feature of complex behavioural domains.

The chapter introduces four interrelated research questions that jointly determine the analytical trajectory of the dissertation: (1) classification and pattern recognition under variation; (2) decision-making under uncertainty; (3) homing as a field-based stress test for explanatory models; and (4) the identification of minimal explanatory assumptions. This structure makes clear that the aim is not to defend a single dominant theory, but to investigate which assumptions prove necessary to understand stable performance. Chapter 1 therefore performs a strictly positioning function. It contains neither a literature synthesis nor a methodological elaboration, but formulates the problem in a manner that justifies the subsequent empirical and methodological steps. The point of departure is clear: the core problem is not the absence of data, but the assessability of explanations when multiple models can accommodate the same behaviour.

Chapter 2 – Literature Review

Chapter 2 surveys the existing literature on classification behaviour and homing navigation in pigeons in order to specify the current state of knowledge and delimit the empirical scope of the research. The chapter does not develop a new theory, but reconstructs provisional answers from the field and identifies where underdetermination occurs.

The literature on classification shows that pigeons can maintain stable performance under systematic variation of stimulus material. Generalisation to new or modified exemplars is well documented empirically. At the same time, these performances do not compel adoption of a single necessary internal explanatory framework. Multiple descriptions of structural sensitivity to stimulus regularities remain compatible with the same behavioural data. Performance sustainability constrains assumptions, but does not eliminate them. Research on decision-making under uncertainty generally shows gradual shifts in performance when information quality varies. All-or-nothing transitions are rare within ecologically plausible ranges. This indicates the simultaneous contribution of multiple information sources, without empirically enforcing the exclusive dominance of any one source. Here too, model selection remains limited for as long as behaviour remains functionally stable. Within the homing literature, magnetic, olfactory, solar-based and visual lines of explanation have been developed, each supported by specific manipulation paradigms. Review studies nevertheless show that comparable behavioural outcomes often remain compatible with multiple models. Manipulations reveal sensitivity, but rarely produce reduction to a single necessary mechanism.

Taken together, the literature reveals a consistent pattern: robust performance sustainability under variation, combined with persistent explanatory pluralism. This defines the experimental scope of the dissertation. Chapter 2 positions the research by specifying what is known, where underdetermination occurs, and which forms of systematic variation are suitable for placing assumptions under pressure without presupposing model reduction.

Chapter 3 – Methodology

Chapter 3 articulates the methodological framework within which the experimental space identified in Chapter 2 is actually exploited. Whereas Chapter 2 showed that multiple explanatory models of classification and homing behaviour can remain simultaneously empirically compatible with stable behavioural outcomes, Chapter 3 operationalises how this compatibility can be addressed systematically and under controlled conditions. The methodology is therefore not a neutral account of implementation, but an explicit translation of an epistemological problem into an empirical design. Central to this design is an assumption-driven, empirical-comparative strategy. Rather than testing a single explanatory model against alternatives, the core assumptions embedded in established models — such as the necessity of specific information sources, the dominance of particular cues or the hierarchical ordering of mechanisms — are made explicit and subjected to controlled variation. The purpose is not to identify a 'winning' model, but to investigate the conditions under which performance sustainability remains intact and which assumptions prove descriptively necessary to characterise that maintenance.

The methodological design is structured around four research questions with distinct statuses. Research Questions 1 to 3 are empirical and generate the data on which the dissertation rests: classification behaviour under systematic stimulus variation (RQ1), homing behaviour under separate variation of navigational cues (RQ2), and homing under combined variation of multiple information sources (RQ3). Research Question 4 has an analytical-theoretical function and organises the empirical findings at the level of assumption structures. This differentiation ensures that the description of empirical patterns and the assessment of models are not prematurely conflated.

Data collection is organised in such a way that behavioural outcomes are recorded under reproducible and controlled conditions. Classification studies employ repeated measurements using systematically varied stimulus sets, while homing research consists of field experiments involving controlled variation of environmental information. A defining feature of the design is its use of gradual, proportional variation. The research seeks to place assumptions under pressure without immediately destabilising the system. Variation therefore functions as an analytical instrument rather than merely as a disturbance. Data analysis is primarily descriptive and comparative. Data are summarised using proportions, means and measures of dispersion, while statistical techniques support comparisons between patterns. Crucially, statistical outcomes are not used as decisive criteria for model selection. The analytical step associated with Research Question 4 focuses on the relationship between empirical patterns and the assumptions presupposed by explanatory models: which assumptions prove unnecessary, which remain compatible, and which are actually addressed within the range investigated?

Validity and reliability are procedurally safeguarded. Internal validity is strengthened through consistent measurement procedures and explicit reference conditions; reliability rests on repeated measurements and transparent recording protocols. Particular attention is also given to interpretative validity: empirical findings and theoretical evaluation are kept strictly separate, ensuring that conclusions remain proportionate to the design. The methodology is also explicitly embedded within ethical constraints. Variations are introduced incrementally and within ecologically plausible limits; extreme or irreversible manipulations are excluded. Ethics therefore functions not as an external assessment imposed afterwards, but as a constitutive condition of the design itself.

Chapter 3 thus forms the methodological link between the literature review in Chapter 2 and the empirical investigations in Chapters 4 to 6. It establishes that underdetermination is not circumvented, but must be investigated systematically.

Chapter 4 – Classification under Controlled Stimulus Variation

Chapter 4 constitutes the first empirical elaboration of the methodological framework described in Chapter 3. Whereas Chapter 2 surveyed the experimental scope surrounding classification ability and Chapter 3 explained how assumptions could be made explicitly addressable, this chapter examines concretely how the classification behaviour of homing pigeons responds to systematic variation in stimulus exemplars. The central question is whether stable classification performance depends on the exact repetition of previously presented stimuli, or whether it is maintained when stimulus configurations change. The experimental design therefore introduces variation in the form, structure and context of visual stimuli within predefined task formats. In addition to training stimuli, new, non-identical exemplars are introduced to investigate the extent to which response distributions generalise.

The results show that classification performance does not collapse abruptly under these variations. The introduction of new exemplars produces measurable shifts in response frequencies, but not a complete disorganisation of behaviour. Performance sustainability is therefore not tied to exact stimulus identity. At the same time, the data do not compel any specific interpretation of the underlying processing mechanism. The empirical patterns are compatible with different descriptions of sensitivity to structural regularities, without any single form of representation being identifiable as strictly necessary. Importantly, the chapter does not claim to demonstrate the existence of classification ability — this is already beyond dispute in the literature — but investigates which assumptions are necessary to describe performance sustainability. The findings constrain strong claims concerning exclusive dependence on specific stimulus presentations, but do not reduce the explanatory space to a single compelling framework. Here too, underdetermination proves to be an empirically demonstrable phenomenon within the range investigated.

Chapter 4 thus demonstrates that stable behavioural outcomes can occur under variation without the underlying assumptions being determined unambiguously.

Chapter 5 – Homing under Variation of Individual Navigational Cues

Chapter 5 constitutes the second empirical pillar of the dissertation and addresses Research Question 2: how does homing behaviour change when individual navigational information sources are systematically varied? Whereas Chapter 4 focused on classification under stimulus variation, the focus now shifts to field-based navigational behaviour under controlled manipulation of sensory information. The point of departure is that existing explanatory models often implicitly assume that specific information sources — magnetic, olfactory, visual or solar-based — are necessary or dominant for successful return. The research design operationalises these assumptions not by isolating a single mechanism, but by incrementally reducing or modifying individual cues within ecologically plausible ranges. Homing performance is measured in terms of return rate, initial orientation deviation and return time.

The results show a consistent pattern of gradual sensitivity. Reduction or manipulation of an individual cue produces measurable shifts in performance indicators, but not a systematic collapse of goal-directed return behaviour. Within the range investigated, no single cue proves strictly necessary in an exclusive sense. At the same time, no cue is without influence: changes in availability correspond to proportional shifts in orientation and flight duration. The findings imply that assumptions concerning strict necessity or hierarchical dominance are not descriptively indispensable within this range of variation. Homing behaviour remains compatible with multiple configurations of information use. Explanatory pluralism is therefore not eliminated but constrained: strong exclusivity claims lose their force without alternative mechanisms being eliminated.

The chapter thus provides empirical evidence that goal-directed navigational behaviour can remain robust under partial uncertainty, while the underlying structure of assumptions is not reduced to a single mechanism.

Chapter 6 – Performance sustainability under Combined Variation

Chapter 6 deepens the analysis of homing behaviour by moving from the manipulation of individual cues to cumulative variation. Whereas Chapter 5 examines sensitivity to individual information sources, this chapter addresses Research Question 3: how does the navigational system behave when multiple navigational cues are simultaneously restricted? The central analytical distinction is between analysis of individual elements and system behaviour under system pressure. Rather than isolating a single cue, multiple dimensions of variation are combined in accordance with predefined configurations. The primary purpose is therefore not to test which mechanism is operative, but to determine whether performance under cumulative uncertainty continues to shift proportionally or instead displays a non-linear transition.

The empirical findings show that combined reduction produces further performance degradation: the dispersion of orientation increases and return times become longer. Crucially, however, no abrupt collapse of homing behaviour occurs within the parameter ranges investigated. Even under increased system pressure, return performance remains above chance level and recognisably goal-directed. This outcome has two implications. First, it supports the interpretation of robustness: the navigational system displays resilience under cumulative uncertainty. Second, explanatory pluralism remains intact. Even under combined pressure, no single explanatory model can be enforced exclusively. Assumptions concerning threshold behaviour or necessary system collapse receive no empirical confirmation within this design, but neither are they excluded in principle beyond the range investigated.

This chapter therefore demonstrates that performance sustainability and explanatory pluralism occur together not only under isolated variation, but also under cumulative pressure. The system degrades proportionally, without compelling reduction to a single mechanism.

Chapter 7 – Answering Research Question 4

This chapter shifts from empirical manipulation to analytical evaluation. Whereas Chapters 4 to 6 documented behavioural outcomes under controlled variation, this chapter addresses Research Question 4: which assumptions about internal processing prove necessary to understand the observed performance, and which can be relinquished without loss of explanatory coherence? The analysis begins with the combined empirical patterns. In both classification (Research Question 1) and homing under individual and combined variation (Research Questions 2 and 3), performance shifts proportionally without abrupt discontinuity within the range investigated. No individual information source proves strictly necessary, and cumulative reduction does not lead to system collapse.

These findings place strong assumptions under pressure. Assumptions concerning exclusive necessity or hierarchical dominance lose their descriptive force when behaviour is maintained despite the reduction of individual or multiple cues. At the same time, the models concerned are not eliminated. The data neither exclude specific mechanisms nor render them unavoidable. The central outcome of this chapter is therefore a differentiation between the statuses of assumptions. Some assumptions prove unnecessary within the chosen design; others remain compatible but are not exclusively confirmed; still others remain empirically undecidable. Explanatory pluralism is therefore not reduced, but explicitly ordered.

The chapter concludes that model assessment in this domain shifts from performance comparison to assumption analysis. Assessability requires assumptions to be made explicit and their descriptive necessity to be tested. Within the ranges of variation investigated, pluralism persists not as a theoretical weakness, but as an empirically bounded finding.

Chapter 8 – Conclusion, Discussion and Further Research

Chapter 8 is primarily concerned with synthesis and reflection. The four research questions are answered individually and subsequently brought together in answering the central research question. With regard to classification behaviour (Research Question 1), performance remains stable under systematic variation of stimulus exemplars. Generalisation occurs without the data compelling reduction to a single necessary representational framework. With regard to homing under individual variation (Research Question 2), return rates and return times shift gradually, without any single cue being identifiable as strictly necessary or exclusively dominant. Under cumulative variation (Research Question 3), performance degradation becomes apparent, but no abrupt collapse occurs within the parameter ranges investigated. Robustness proves bounded, but persistent. On this basis, Research Question 4 is answered: explanatory models remain difficult to eliminate in relation to one another for as long as they remain compatible with observed performance sustainability. Making assumptions explicit narrows the scope for strong exclusivity claims, but does not lead to reduction to a single dominant model. Explanatory pluralism thus emerges as an empirically bounded feature of the relationship between behavioural stability and explanatory structure.

The discussion qualifies this outcome. Underdetermination is not presented as a trivial property of complex systems, but as a finding within specific ranges of variation and particular behavioural measures. Internal validity is strong within the chosen design, but the scope of the findings is constrained by ethical proportionality, measurement resolution and population variation. The dissertation concludes that reliable behavioural performance is possible without enforceable explanatory reduction. Stability and underdetermination prove not to be opposites, but simultaneously occurring features of the same system. The epistemological implication is formulated proportionately: within this domain and under these conditions, performance sustainability does not coincide with explanatory reduction.

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Chapter 1 – Introduction: Reliable Performance, Inadequate Explanations and the Need for Repositioning

1.1 Reliable Performance and Inadequate Explanations

Within the natural sciences, systems frequently function consistently and reproducibly while explanations of that functioning remain incomplete or inadequate. In this dissertation, explanation does not refer to a complete mechanistic reconstruction, but to a coherent set of assumptions that renders observed behaviour plausible, replicable and epistemologically bounded. Explanations may, in this sense, be adequate to varying degrees: they may explain much without explaining everything. Behaviour in particular creates a tension between what can be observed reliably and what can be explained adequately. Complex behaviour may arise through multiple causal pathways, context-dependent processes and redundant sources of information. In such cases, the level of explanation often lags behind the level of performance: it is possible to describe accurately that a system performs, while understanding only partially how that performance is produced. The existence of this tension does not imply that performance is accidental, but that existing explanatory frameworks may have been formulated too narrowly, too specifically or too optimistically (Tinbergen, 1963; Mayr, 1982).

This tension between reliable performance and explanatory univocality is particularly apparent in research on navigation in homing pigeons. Recent review studies indicate that homing behaviour arises through a combination of olfactory information, solar orientation, magnetic sensitivity and visual landmarks, with the relative contribution of individual cues depending on context and experience (Mouritsen, 2018; Hough, 2022). Within the conventional experimental range, none of these information sources can be regarded as exclusively or universally necessary; reducing or manipulating a single cue generally produces a gradual shift in performance rather than a complete disorganisation of behaviour. This creates an empirical domain in which multiple explanatory frameworks remain simultaneously plausible. A comparable situation occurs in research on visual categorisation in pigeons. Pigeons display robust classification performance under a wide range of stimulus variations, while debate persists concerning the nature of the underlying representations and decision processes (Wasserman, 2024; Pusch et al., 2022). The performance is reproducible and quantifiable, but theoretical interpretations vary between exemplar-based, prototype-based and integrative approaches. Here too, performance sustainability does not automatically result in model elimination. This body of research indicates that the tension between reliable behavioural outcomes and multiple explanatory possibilities is not an abstract philosophical problem, but a concrete feature of contemporary research on avian navigation and cognition.

This research proceeds from the assumption that this tension is not an anomaly, but a structural feature of research on complex behaviour. The central question is therefore not whether explanations are possible, but which assumptions are necessary to understand reliable performance and which assumptions can be relinquished without diminishing explanatory capacity. Research on pigeon navigation encompasses several explanatory traditions that have not merely been complementary, but have historically also advanced competing claims. Olfactory map hypotheses, magnetic map models and landmark-based route approaches have each experienced periods in which they were presented as primary or decisive. Integrative models seek to overcome these tensions by incorporating multiple information sources into a single framework, but these approaches also differ in the extent to which they assume necessity, dominance or hierarchical ordering. The existence of multiple empirically supported but theoretically non-equivalent models demonstrates that the tension between reliable performance and explanatory univocality is not a rhetorical construct, but an actual structural feature of the research domain. In this dissertation, an explanatory framework is regarded as problematic when it requires assumptions that are not empirically compelled within the experimental range investigated, and as provisionally adequate when it can describe the same level of performance using less demanding assumptions.

1.2 Decision-Making under Structural Uncertainty

Behaviour occurs in environments in which information is rarely complete or unambiguous. In this dissertation, uncertainty refers to conditions in which relevant information is intrinsically incomplete, susceptible to noise or mutually conflicting. Uncertainty is treated not as a temporary disturbance, but as a structural feature of natural environments.

In this context, decision-making refers to the production of behavioural choices on the basis of available information, without presupposing optimality. In contrast to models based on maximum accuracy or complete information processing, this research adopts a functional approach: behaviour is considered successful when it is sufficiently adequate to produce consistent performance. Variation and error tolerance are not treated as failures, but as possible conditions for robust functioning (Simon, 1956; Gigerenzer et al., 1999).

This approach is consistent with research traditions in which natural decision-making is understood as the outcome of heuristic processes and redundant cue integration. From this perspective, explanatory models centred on optimality risk underestimating structural uncertainty and reducing behaviour to idealised schemes with limited explanatory power outside natural contexts (Gigerenzer & Selten, 2001).

1.3 Homing Pigeons as a Biological Model and Epistemic Point of Reference

This research selects homing pigeons, selectively bred varieties of the rock dove (Columba livia domestica), as its object of study. Through prolonged artificial selection, these birds have been optimised for consistent return to a fixed home loft after controlled displacement. In this dissertation, homing pigeons explicitly do not refer to ordinary feral urban pigeons, but to birds forming part of a well-documented research tradition in which performance has been established systematically, reproducibly and under field conditions.

Contemporary research moreover treats the homing pigeon not only as a traditional model of navigation, but also as a system in which multiple information sources are integrated across changing contexts. Recent review studies emphasise that homing performance arises through the interaction of olfactory signals, solar orientation, magnetic sensitivity and visual landmark information, with the relative contribution of these sources depending on experience, geographical familiarity and environmental conditions (Mouritsen, 2018; Hough, 2022). This context-sensitive integration makes the model particularly suitable for research on behavioural stability under variation, because no individual cue can be regarded as exclusively explanatory within the conventional experimental range.

Recent research on visual cognition in pigeons has also confirmed that their classification performance is not limited to simple stimulus discrimination, but extends to complex categorisation problems involving varying stimulus configurations (Wasserman, 2024; Pusch et al., 2022). Pigeons are capable of producing consistent decisions when confronted with changing exemplars and partial information, without requiring explicit assumptions about language-like representations or semantic understanding. This combination of field-based navigational robustness and experimentally demonstrable classification capacity makes the model particularly suitable, from an epistemic perspective, for analysing reliable performance under conditions of uncertainty.

The scientific value of homing pigeons as a model organism is not confined to their homing capacity, but derives from a broader behavioural profile. In addition to their navigational performance under field conditions, experimental research has demonstrated that pigeons possess a robust capacity for pattern recognition and classification. They can discriminate between complex visual and spatial stimulus configurations, generalise to new cases and respond consistently under variation and noise, without requiring assumptions about semantic understanding, explicit concept formation or internal symbolic representations (Herrnstein et al., 1976; Cook, 2001).

Pattern recognition is therefore understood in this dissertation as a behavioural capacity: the consistent discrimination and use of regularities in the environment, as inferred from observable performance. This definition avoids both anthropomorphism and speculation about internal mental states and is consistent with a functional approach to behaviour. It is precisely this combination of reliability under field conditions and experimentally demonstrable classification ability that enables the homing pigeon to function as a scientific point of reference for broader questions concerning reliable performance in the absence of complete explanatory transparency. Without advancing technological claims, this biological model permits reflection on a problem that also arises in other scientific and societal domains: how should systems be treated when they demonstrably function while their internal operation remains only partially accessible? The analogy is not intended to transfer biological insights to technology, but to serve as an epistemic mirror demonstrating that functioning without understanding is not an exceptional but a structural phenomenon.

1.4 The 'Arctic Night' as a Constructed Limit Case

To make implicit assumptions in explanatory models explicit, this dissertation introduces the phrase 'homing pigeons in the Arctic night' as a constructed limit case. A limit case is understood here as an analytical device that does not describe an ecologically realistic scenario, but serves to test explanations under extreme, simplified conditions. The allegorical function of this thought construct lies in simultaneously problematising several presumed sources of information. By envisaging a situation in which daylight is absent and particular orientation signals are unreliable, it becomes possible to identify the tacit assumptions that explanatory models make about necessary cues. The value of this approach lies not in its empirical plausibility, but in its conceptual precision: it compels explicit identification of what explanations actually require.

Comparable limiting approaches are used in research on animal navigation when specific information sources are experimentally reduced or manipulated. Studies of magnetic disruption, olfactory deprivation and visual occlusion show that behavioural change is often proportional and depends on the availability of alternative information sources (Mouritsen, 2018; Hough, 2022). Explicitly reasoning in terms of limit cases is consistent with this experimental practice: by rendering several cues problematic at the same time, it becomes possible to identify which assumptions concerning necessity and dominance are genuinely indispensable. The 'Arctic night' therefore functions not as an ecological prediction, but as an analytical device for examining how behaviour changes when redundancy is placed under pressure. In systems in which multiple sensory contributions jointly generate a stable outcome, reducing one or more components may produce gradual degradation rather than abrupt collapse. This form of robustness through multiple integration has been described in the perception literature as a feature of systems that combine information sources into a functionally stable output (Ernst & Bülthoff, 2004). The limit case makes it possible to treat such robustness not as self-evident, but as a testable assumption.

The use of idealisations and limiting cases is an established instrument in the natural sciences for disciplining models and testing assumptions (Hempel, 1965; Weisberg, 2007).

1.5 Homing: Definition and Function in This Research

In this dissertation, homing refers to the performance whereby a homing pigeon, after being displaced along an unfamiliar route, independently returns to a fixed home loft. This definition is performance-oriented and in itself says nothing about the underlying mechanism. Homing is not treated here as synonymous with navigation, but as an outcome that may integrate multiple processes. Within the design of this research, homing functions as a subsequent stress test for explanatory models. Because homing imposes particularly demanding requirements of consistency and robustness, it can be used to assess which explanatory assumptions remain tenable under challenging conditions. By treating homing not as the point of departure but as a test, the research avoids being reduced to a single mechanistic problem.

1.6 Research Questions and Structure of the Dissertation

Against the background of the problem outlined in this chapter, the dissertation addresses the following central research question: 'To what extent can homing pigeons make consistent and reliable behavioural decisions under structural uncertainty, without explicit semantic understanding or transparent internal representations?' This central question is elaborated through the following research questions, which jointly determine the analytical trajectory of the study:

Research Question 1 (Pattern Recognition and Classification): 'Which forms of pattern recognition and classification do homing pigeons display when confronted with variable and noisy stimuli, and to what extent does this performance remain stable when information is incomplete or conflicting?'

Research Question 2 (Decision-Making under Uncertainty): 'How do homing pigeons integrate fragmentary and partly conflicting information into behavioural decisions that remain functionally reliable, without presupposing optimality or complete information processing?'

Research Question 3 (Homing as an Ultimate Field Test): 'To what extent does field-based homing behaviour in homing pigeons function as a stress test for explanatory models that assume explicit internal representations when dominant information sources are restricted or unreliable?'

Research Question 4 (Minimal Explanatory Assumptions): 'Which assumptions about internal processing prove necessary to understand the observed performance, and which assumptions can be relinquished without loss of explanatory coherence?'

The structure of the dissertation follows this set of questions. Chapter 2 reviews the existing literature and formulates provisional answers to these research questions insofar as the current state of research permits, while explicitly identifying where explanations remain incomplete or inadequate. Chapter 3 then justifies the methodological choices made in this research and describes how these lacunae are systematically addressed through analysis of existing empirical material and reductive explanatory strategies.

Chapter 2 – Literature Review

2.1 Pattern Recognition and Classification in Pigeons

This section provides a provisional answer to Research Question 1: ‘Which forms of pattern recognition and classification do pigeons display, and to what extent does this performance remain stable under variation and noise?’ In this dissertation, pattern recognition is understood in strictly behavioural terms: the reproducible differentiation and grouping of stimulus configurations on the basis of observable regularities, as inferred from choice or response outcomes. This definition presupposes neither language nor semantic understanding, nor explicit ‘concepts’ in the human sense; it is compatible with functional explanations that relate performance to stimulus sensitivity and learning history.

The empirical basis for such capacities in pigeons has been investigated over an extended period. A frequently cited point of departure is the work of Herrnstein and colleagues, in which pigeons learned to discriminate photographs belonging to natural classes, such as trees, water and people, and classified novel, untrained images almost as accurately as the training images (Herrnstein et al., 1976). This type of result shows that performance cannot be reduced to memorisation of a small set of stimuli: generalisation occurs across variation within a class.

Subsequent research has broadened the scope of pigeon categorisation. Later photographic paradigms have shown that pigeons can learn multiple categories in parallel and continue to generalise when presented with novel exemplars from familiar categories (Wasserman et al., 2014). Research on object–picture equivalence has also examined the extent to which pigeons recognise the ‘same’ object when its mode of representation changes, for example from a real object to an image, thereby making classification less dependent on one specific stimulus form (Watanabe, 1993). Research using artificial, multidimensional stimuli further shows that categorisation in pigeons is not confined to ecologically ‘natural’ images, but also occurs when the task requires structural integration of multiple stimulus dimensions (Berg et al., 2011).

What matters for this chapter is not any single paradigm, but the convergence of findings: across diverse task types and stimulus sets, pigeons repeatedly demonstrate classifications that withstand variation, noise and novel exemplars. Review and synthesis articles therefore describe the pigeon as a frequently used model in avian visual cognition and categorisation, partly because a cumulative research tradition has established consistent performance (Cook, 2001; Qadri & Cook, 2015). More recent contributions are consistent with this literature in showing that even complex category structures can be learned and in examining the extent to which relatively simple learning mechanisms may already be sufficient to account for them (Turner & Wasserman, 2023). Finally, work explicitly building on the Herrnstein paradigm indicates that its central findings — categorisation accompanied by generalisation — have become firmly established in the subsequent literature (Edwards, 1987).

Provisional answer to Research Question 1. The literature shows that pigeons (i) can recognise patterns and classify stimuli reproducibly, (ii) generalise to novel exemplars and maintain performance under variation in relevant paradigms, and (iii) do not require explanations invoking semantic understanding or linguistic representations, provided that those explanations remain functional and behavioural in formulation.

At the same time, a deliberate lacuna remains that is not addressed here. The literature primarily documents that categorisation and generalisation occur, but specifies less precisely which assumptions are minimally necessary to sustain such performance, for example which stimulus features, learning conditions or forms of cue use are required. Moreover, the connection to functioning under field conditions — where circumstances are richer, less orderly and less controlled — is often made only implicitly. This lacuna is synthesised explicitly in §2.4 and subsequently provides a direct rationale for the reductive, assumption-oriented approach adopted in Chapter 3.

2.2 Decision-Making and Cue Integration under Uncertainty

This section provides a provisional answer to Research Question 2: 'How do pigeons make decisions when confronted with incomplete, noise-prone or conflicting information, and to what extent do their behavioural outcomes remain functional under such conditions?' Decision-making here refers to the production of observable behavioural choices on the basis of available signals, or cues, without assuming that these choices are optimal or based on complete information.

A broad range of experimental studies shows that pigeons use multiple information sources simultaneously in their behaviour. These cues may differ in kind, including visual features of the environment, magnetic information and other contextual signals. The central observation is that none of these cues appears individually necessary for goal-directed behaviour to occur; instead, they are integrated in the production of decisions (Wiltschko & Wiltschko, 1995; Wallraff, 2005).

This integration process becomes visible in so-called cue-conflict experiments. In such designs, two or more cues are manipulated so that they provide mutually conflicting information. When pigeons are tested under these conditions, they generally do not display an abrupt loss of directed behaviour. Instead, behavioural choices remain goal-directed while variation in outcomes increases. This may be expressed, for example, in a wider dispersion of selected directions or routes, both between individual birds and across repeated measurements of the same bird (Wiltschko & Wiltschko, 1995).

A comparable pattern is observed when individual cues are selectively disrupted or removed. When a previously dominant information source is temporarily rendered unreliable, behavioural precision decreases, but without producing complete disorientation or randomness. The change in performance is gradual: behaviour shifts, compensates or becomes more variable, while retaining its functional character (Biro et al., 2004; Gagliardo et al., 2009). This indicates redundancy in the decision-making process, with multiple cues partially substituting for one another depending on context and availability.

Within this field of research, behavioural variation is therefore not regarded merely as measurement noise, but as a structural feature of decision-making under uncertainty. Variation reveals how different information sources are used and reweighted when conditions change. In this sense, the dispersion of behavioural outcomes itself provides information about the underlying decision-making process, rather than constituting something that should be filtered out.

These empirical findings are consistent with functional approaches to decision-making that dispense with normative criteria of optimisation. Within such frameworks, behaviour is described as adequate given the constraints of the environment and the available information. Decision-making is assessed not in terms of maximum accuracy, but in terms of the capacity to remain goal-directed across varying circumstances (Simon, 1956; Gigerenzer et al., 1999). Applied to research on pigeons, this means that consistent behavioural outcomes can be understood without assuming either that all relevant information is used or that an optimal solution is pursued.

A comparative reading of the literature shows that these patterns recur across different experimental designs and cue types. The integration of multiple cues, context-dependent shifts in weighting and the maintenance of functional outcomes under disruption are repeatedly observed across diverse studies. At the same time, explanatory models often remain tied to specific tasks or cue configurations. They describe that weightings change, but rarely make explicit which assumptions are necessary to explain those changes.

Provisional answer to Research Question 2. The existing literature shows that pigeons (i) make decisions by integrating multiple information sources, (ii) continue to act in a goal-directed manner under conditions of uncertainty, with gradual changes in performance, and (iii) do not require decision-making to be optimal or based on complete information for these outcomes to occur.

At the same time, a clear lacuna remains. Existing models do not specify with sufficient precision which cues are necessary and which are substitutable, or how context-dependent weighting is produced. Decision-making is described in terms of behavioural outcomes and shifts, but is not reduced to minimal assumptions. This lacuna is brought together in §2.4 and, in conjunction with the findings from §§2.1 and 2.3, provides the rationale for the methodological elaboration in Chapter 3.

2.3 Navigation and Homing: Classical Explanatory Models

This section formulates a provisional answer to Research Question 3: 'To what extent can the homing behaviour of homing pigeons be understood on the basis of existing explanatory models, and what limitations do these models display when homing is treated as field-based performance under changing conditions?' Homing is defined here as the observable outcome whereby a pigeon, after displacement along an unfamiliar route, independently returns to a fixed home loft. This definition is performance-oriented and contains no assumptions about underlying mechanisms.

Several explanatory traditions have been developed in the literature to account for homing performance. One classical approach concerns sun-compass models, in which time-compensated orientation based on the position of the sun is central. In these models, internal time information contributes to deriving direction, while disturbances in time perception may produce systematic directional deviations (Wiltschko & Wiltschko, 1995). In parallel, magnetic orientation has been investigated, whereby information from the Earth's magnetic field is used to determine direction. Experimental manipulations of magnetic signals show that this type of information may contribute to orientation, but is not necessary in every context (Wiltschko & Wiltschko, 1995).

Another explanatory tradition concerns olfactory map hypotheses, which assume that geographical localisation is partly achieved through spatial patterns in odour gradients. Within this approach, homing is understood as the combination of directional information with location-specific olfactory cues, while disruption of olfactory information may lead to altered performance (Wallraff, 2005). Extensive research has also examined the use of visual cues and imprinting, particularly landmark learning and recognition of landscape configurations in the vicinity of the home loft. These studies show that visual information may contribute to route-based orientation and to the fine-tuning of the final stages of return (Biro et al., 2004).

More recent syntheses bring these separate explanatory traditions together in multi-cue integration models, which assume that pigeons use multiple information sources simultaneously and weight them in a context-dependent manner. From this perspective, no single cue is individually necessary or sufficient; homing performance is understood as the outcome of combined and partly redundant information processing (Wallraff, 2005).

A comparative reading of this literature shows that the diversity of explanatory models coincides with a high degree of performance sustainability under varying conditions. Homing performance often persists when individual cues are disrupted or manipulated. At the same time, the different models employ divergent assumptions and levels of explanation, making them difficult to assess in relation to one another. Studies demonstrate that performance is maintained, but provide less clarity about which assumptions are necessary to understand that maintenance.

Provisional answer to Research Question 3. The existing literature shows that homing behaviour may be supported by multiple types of information, including solar, magnetic, olfactory and visual cues, and that integration of these sources contributes to performance sustainability under disruption. No individual explanatory model, however, is sufficient on its own to account for all observed homing performance when homing is treated as a field-based stress test.

At the same time, a clear lacuna remains. The literature does not specify with sufficient precision which assumptions are necessary for maintaining homing performance and which assumptions are contingent or context-dependent. Explanations describe multiple possible contributions, but rarely delimit their own scope. This lacuna is brought together explicitly in §2.4 and forms the basis for the methodological approach developed in Chapter 3, which examines how performance sustainability can be understood using the most limited possible set of assumptions.

What is striking in these review studies is not only the robustness of homing behaviour under varying conditions, but also the absence of elimination between explanatory models. Navigational hypotheses based on geomagnetic information, olfactory cues, solar or light-based orientation and visual landscape recognition each remain empirically compatible with the observed maintenance of performance, without systematically displacing one another. In this domain, explanations appear to function not as competing alternatives, but as cumulative perspectives capable of accommodating the same behavioural outcome. Homing behaviour therefore does not constitute a case in which increasing empirical refinement automatically leads to explanatory reduction, but rather one in which explanatory pluralism persists despite decades of research.

2.4 Assessability of Sustained Performance

This section addresses Research Question 4 at a theoretical level. The question is as follows: How can sustained performance in pigeons be investigated methodologically when multiple explanatory models accommodate the same behaviour, and which assumptions must be made explicit in order to render those models assessable in relation to one another? Research Question 4 is not concerned with selecting a correct or dominant explanation of homing behaviour, but with determining how explanations can be assessed in a domain in which multiple causal models remain empirically compatible with the same behaviour. The answer to this research question is therefore primarily theoretical in nature. It seeks to clarify which assessment criteria are meaningful in a context in which sustained performance does not distinguish between explanations and in which explanatory pluralism does not automatically disappear as empirical detail increases.

This research question differs in kind from the preceding questions. Whereas the first three research questions concern observable behaviour and empirical performance patterns, Research Question 4 addresses the conditions under which knowledge claims about that behaviour can be assessed. The primary concern is not the behaviour itself, but the status and comparability of the explanations advanced to account for it.

Across a range of scientific domains, stable performance under varying conditions is known to coexist with explanatory pluralism. Where behavioural outcomes are reproducible, it is often possible to formulate multiple explanatory models that remain compatible with the same empirical data. This applies not only to biological behaviour, but also to other forms of system behaviour in which consistent output is produced under variable conditions, including automated and modelled behaviour. The presence of multiple compatible explanations does not in itself constitute an anomaly, but may be a structural feature of complex systems.

The resulting epistemological problem concerns the assessability of explanatory models. When different models accommodate the same sustained performance, empirical compatibility alone provides no criterion for ranking them in relation to one another. The focus then shifts from the empirical adequacy of individual explanations to the nature and status of the assumptions on which they rest. As long as those assumptions remain implicit, or are justified only in relation to particular contexts, it remains unclear which elements of an explanation are necessary to account for sustained performance and which are merely incidental or substitutable.

This situation is compounded by the fact that explanatory models often operate at different levels. Some models focus on specific information sources, whereas others address integration processes or contextual influences. Although each model may clarify a particular aspect of the behaviour, together they generate a proliferation of explanatory frameworks without clarifying how those frameworks relate to one another. The problem is therefore not that the explanations are empirically incorrect, but that they are insufficiently bounded epistemologically to permit comparative assessment.

This persistent explanatory pluralism cannot be understood solely as a consequence of incomplete knowledge or methodological limitations. In the case of homing behaviour, it is plausible that it also arises from properties of the biological system itself. Navigational behaviour in homing pigeons is redundantly organised: multiple information sources can support the same functional outcome. At the same time, experience and context affect the weighting and use of available cues. In such systems, the existence of multiple simultaneously valid explanations need not constitute a temporary stage, but may instead be a structural feature of the relationship between behaviour and explanation. This implies that explanatory pluralism in homing cannot necessarily be eliminated through further empirical refinement within a classical eliminative framework.

Research Question 4 articulates this problem explicitly. It shows that further empirical refinement within existing frameworks does not automatically produce greater theoretical clarity as long as the assumption structures of explanatory models are not systematically made explicit. The absence of such explication limits the assessment of explanations, not because sustained performance has been insufficiently documented, but because the relationship between explanatory assumptions and that sustained performance has been insufficiently examined.

This section is confined to formulating the epistemological problem at a theoretical level. It offers no synthesis of the preceding sections and presents no methodological solution. In this way, the position of Research Question 4 within the research as a whole is delimited. The question is articulated here as a theoretical problem; Chapter 3 develops possible methodological strategies for making assumptions explicit and rendering explanatory models assessable in relation to one another.

2.5 Field Studies of Homing Pigeons: Empirical Scope for Investigation

Research on homing behaviour in homing pigeons rests on a well-developed experimental infrastructure in which both the recording and manipulation of navigational behaviour are technically feasible. This instrumentation is relevant because it demonstrates that variation in individual information sources need not remain a merely theoretical assumption, but can be realised and quantified empirically.

Recording navigational behaviour. The introduction of lightweight GPS loggers has made it possible to record individual flight paths at high resolution. These data permit analysis of departure orientation, course deviation, speed, detours and route recapitulation (Biro et al., 2004; Guilford & Biro, 2014). This technology makes it possible to assess behavioural change under variation not only in terms of return rate, but also at the level of trajectory structure and initial heading. Navigational behaviour thereby becomes a quantifiable variable rather than a global outcome measure.

Manipulation of individual information sources. Alongside recording techniques, a range of manipulations has been developed to investigate the contribution of specific navigational cues. Olfactory information can be temporarily disrupted through controlled deprivation or disorientation protocols (Wallraff, 2005). Magnetic sensitivity has been investigated experimentally by attaching small magnets or using coil configurations that alter local magnetic-field conditions (Wiltschko & Wiltschko, 2005; Mouritsen, 2018). Solar orientation can be affected through clock-shift experiments, while visual information can be manipulated experimentally by releasing birds in familiar or unfamiliar terrain or by masking landmarks (Guilford & Biro, 2014). Such interventions generally produce measurable shifts in orientation and route patterns without necessarily causing complete behavioural disorganisation under all conditions. The literature therefore shows that individual information sources can be isolated experimentally, but are not necessarily exclusively explanatory.

Cue weighting and context-dependent integration. Part of the recent literature approaches navigation in terms of the context-dependent integration of multiple information sources. From this perspective, cues are not treated solely as present or absent, but as being weighted variably in relation to experience, geographical familiarity and environmental conditions (Mouritsen, 2018; Hough, 2022). Experimental reduction of one cue may be accompanied by a shift in the relative contribution of other cues, without requiring the assumption of a fixed hierarchical ordering. This approach shifts attention from binary necessity to gradual contribution. Manipulation of information sources is then understood not primarily as the disabling of a mechanism, but as a change in informational value within an integrated system.

The control-dial model as an experimental abstraction. The instrumentation described above can be abstracted in terms of adjustable parameters. Olfactory availability, magnetic consistency, solar information and visual recognition constitute separate dimensions along which experimental variation is possible. Each of these dimensions can, within certain limits, be increased, reduced or disrupted while other conditions remain constant. This parametric manipulability can be conceptualised as a configuration of control dials: individual information sources function as adjustable variables whose relative contribution to the behavioural outcome can be varied systematically. The purpose of such variation is not to simulate ecologically extreme situations, but to investigate behavioural change under controlled shifts in informational value. The control-dial model is introduced here not as a biological theory, but as a methodological abstraction of existing experimental practice. The literature shows that individual navigational cues are technically manipulable and quantifiable. This creates a research domain in which variation along multiple dimensions is possible without rendering the behavioural outcome unmeasurable.

Methodological implication. The experimental infrastructure surrounding homing-pigeon navigation makes it possible to address assumptions concerning necessity, dominance and integration not only conceptually, but also through parametric variation. The fact that such variation frequently produces gradual rather than abrupt behavioural change in the literature is not itself a conclusion, but an empirical point of departure. It shows that the question of explanatory adequacy can be linked to the systematic manipulation of informational dimensions. In this sense, research on navigation in homing pigeons provides an experimental framework within which behavioural stability and variation can be investigated under controllable conditions. This manipulability forms the methodological basis for the empirical chapters that follow.

2.6 Synthesis: Sustained Performance, Explanatory Pluralism and Empirical Scope for Investigation

This chapter has sought to organise existing knowledge of homing behaviour in homing pigeons along three interrelated lines: empirical performance, explanatory frameworks and the conditions under which those explanations can be assessed. Each of the preceding sections has examined a different aspect of this relationship, without seeking reduction to a single explanatory model or a conclusive mechanism.

Sections 2.1–2.3 established that homing behaviour is characterised by robustly sustained performance. Homing pigeons are capable of returning in a goal-directed manner across a range of contexts, both under controlled conditions and under variation in the field. This performance remains substantially intact despite changes in distance, context and the availability of information, indicating a form of behavioural stability that is well documented empirically.

At the same time, this sustained performance was shown to coexist with explanatory pluralism. Multiple explanatory models exist for the same behavioural outcomes, making different assumptions about information sources, integration processes and contextual factors. These models are generally empirically compatible with the observed performance, but differ in their underlying assumptions and in the ways in which they conceptually organise behaviour.

In §2.4, this situation was explicitly problematised. The central problem was identified not as a lack of empirical data, but as the assessability of explanatory models when they accommodate the same sustained performance. As long as assumptions remain implicit and are not addressed systematically, no clear criterion exists for comparing or delimiting explanations. This is an epistemological problem that cannot be resolved solely through further empirical refinement within existing frameworks.

Section 2.5 subsequently identified the empirical scope for addressing this problem more closely. By treating field studies as a context in which ceteris paribus variation can be introduced gradually and iteratively, it specified the procedural dimensions along which the assumptions of explanatory models can be addressed indirectly. The identified control dials — spatial organisation, the configuration of sensory information sources, temporal structure and procedural alignment — do not constitute explanations, but opportunities for systematic variation with interpretative relevance.

Taken together, these sections show that the central challenge is not to establish that homing pigeons display homing performance, but to develop a research strategy that renders explanations of that behaviour assessable in relation to one another. Chapter 2 has articulated this challenge by documenting performance, making explanatory pluralism explicit and organising the available empirical scope for investigation. It thereby prepares the transition to a methodological elaboration in which assumptions are made explicit and can be addressed systematically.

Chapter 3 builds on this foundation by examining how the empirical variation identified in this chapter can be incorporated into a coherent research design, with the aim of delimiting explanatory models without denying the sustained nature of the performance itself.

Chapter 3 – Methodology

This chapter describes the methodological design through which the behaviour of homing pigeons examined in this dissertation is studied empirically. The chosen research strategy is tailored to the nature of the research object and to the problem identified in Chapter 2: that multiple explanatory models of homing behaviour and classification ability may remain simultaneously compatible with the empirical evidence.

Rather than adopting a hypothesis-testing or explanation-selective approach, this research employs an assumption-driven, empirical-comparative strategy. Central assumptions within established explanatory models (Mayo, 2018; Woodward, 2003) are made explicit and subsequently addressed systematically through controlled variation of relevant conditions. The aim is not to identify a single decisive cause, but to investigate the conditions under which behavioural performance remains stable, changes or loses its explanatory coherence.

The empirical studies in this dissertation combine controlled variation with ecologically plausible conditions. Variation is treated not merely as a disturbance, but as an analytical instrument for identifying which features of the environment, task and organism are functionally relevant to behaviour. This approach is consistent with manipulation-based conceptions of causal testing. It makes it possible not only to describe performance outcomes, but also to investigate the assumptions underlying established explanatory models. The methodological focus therefore lies on the relationship between behavioural stability and explanatory structure, rather than on causal selection or optimisation.

The chapter is structured as follows. It first explains how the individual research questions are positioned methodologically and which assumptions are central to each. It then describes how data collection and data analysis are designed to test these assumptions empirically, with attention to proportional burden and ethical constraints. Finally, it explains how validity and interpretative restraint are safeguarded, ensuring that conclusions remain within the limits imposed by the research design.

3.1 Research Design and Data Collection

The empirical design of this study is aimed at the systematic investigation of behaviour under controlled variation. Across all sub-studies, the point of departure is not a single pre-assumed dominant explanatory factor, but the possibility that homing behaviour and classification performance may result from multiple mechanisms operating simultaneously. Data collection is therefore organised so that performance can be observed under varying conditions, with specific features of the stimulus environment and navigational context being deliberately manipulated.

For the study of pattern recognition and classification, repeated behavioural measurements are conducted using visual stimulus sets that vary systematically in form, structure and context. This design makes it possible to examine the extent to which classification behaviour depends on superficial stimulus features or on sensitivity to more abstract regularities. The preservation of performance when new or modified stimuli are introduced constitutes a crucial observation, as it provides insight into the degree of generalisation.

The study of homing behaviour is conducted under field conditions in which homing pigeons are released under carefully controlled variation in environmental information. Depending on the research question, manipulations are applied either separately or in predetermined combinations, allowing both cue-specific sensitivity and performance retention under cumulative information restriction to be examined. Distances and conditions are selected so as to be both ecologically realistic and proportionate in terms of burden, in accordance with established ethical guidelines for animal research.

Across all sub-studies, data collection is directed towards recording performance outcomes, consistency across repeated trials, and changes under variation. Data collection is explicitly not organised as a search for maximal effects. Instead, emphasis is placed on identifying patterns of stability and change that provide insight into the conditions under which behaviour is maintained.

3.2 Research Questions and Research Approach

This research is organised around four research questions, each of which makes a distinct but related contribution to addressing the central problem: that multiple explanatory models of homing behaviour and classification ability in homing pigeons may remain simultaneously compatible with the empirical evidence. This problem of underdetermination and unconceived alternatives has been analysed systematically in more recent philosophy-of-science literature (Stanford, 2006). The research approach is therefore directed not towards selecting a single dominant explanation, but towards making the assumptions on which explanatory models rest explicit and empirically addressable.

The research questions differ in methodological status. Research Questions 1 to 3 are empirical and generate the data on which the study rests. Research Question 4 is analytical-theoretical and organises these empirical findings at the level of explanatory structures. In all four research questions, the primary concern is not performance as such, but the conditions under which sustained performance remains possible.

3.2.1 Research Question 1: Pattern Recognition and Classification

The first research question concerns the classification and pattern-recognition capacities of homing pigeons. Research in this domain explicitly rests on the assumption that classification performance does not arise exclusively from memorisation of individual stimuli, but is based on recognition of structural regularities. It is additionally assumed that such performance generalises to novel exemplars within a category and that sustained performance indicates stable internal response strategies or representations.

The research approach to this question is designed to make these assumptions explicitly addressable. This is achieved by investigating classification behaviour under systematic variation of stimulus form, complexity and presentation, and by introducing novel, untrained stimuli within familiar categories. The aim is not to establish that pigeons classify, but to determine which assumptions are necessary for classification performance to be sustained.

3.2.2 Research Question 2: Homing under Variation of Individual Navigational Cues

The second research question concerns homing behaviour under variation of individual navigational cues. Explanatory models in this domain explicitly assume that specific sensory information sources — including magnetic, olfactory, visual and solar-related cues — are functionally necessary for successful navigation. Many models additionally assume that disruption of a dominant cue leads to systematic performance loss and that recovery of performance indicates compensation by alternative mechanisms.

The research approach to this question is directed towards explicitly testing these assumptions without determining in advance which cue should be dominant. By studying homing behaviour under controlled variation of individual forms of sensory availability, the research examines the extent to which assumptions concerning necessity, dominance and compensation remain empirically tenable.

3.2.3 Sustained Performance under Combined Variation

For the third research question, data collection consists of homing measurements under predetermined configurations in which two or three navigational cues are manipulated simultaneously. These configurations represent different levels of cumulative information restriction, but are not necessarily implemented in ascending order. Because the same pigeons undergo multiple conditions, the order of implementation may affect performance through experience, habituation, fatigue, or changes over the course of the study period. The conditions are therefore not administered to all animals in the same sequence. The thirty pigeons are divided into five groups of six animals, with each group undergoing a different sequence of conditions. Consequently, each condition occurs equally often as the first, second, third, fourth and fifth release. Condition, distance and sequence position are therefore not systematically confounded.

The research approach for this question is designed to confront these assumptions explicitly with situations in which multiple variations are applied simultaneously. By tracking changes in performance under gradually increasing system pressure, the study examines whether explanatory pluralism persists only under limited variation, or also under conditions in which several assumptions are placed under pressure at the same time.

3.2.4 Research Question 4: Assessability of Explanatory Models

The fourth research question concerns the assessability of explanatory models under persistent pluralism. Theoretical evaluation of explanatory models explicitly presupposes that explanations can be compared on the basis of performance outcomes, that alternative explanations can be eliminated through sufficient empirical refinement and that explanatory pluralism constitutes a temporary stage.

This research question is not investigated empirically, but answered analytically through synthesis of the empirical findings from Research Questions 1 to 3. The research approach focuses on making assessment criteria explicit and on determining which assumptions can be eliminated without undermining sustained performance, and which remain necessary to explain the observed behavioural stability.

Taken together, the four research questions make it possible to investigate homing behaviour and classification ability without reducing explanatory pluralism to a deficiency of the research design. Instead, pluralism is treated as an empirically and epistemologically relevant phenomenon whose underlying assumptions are explicitly identified and systematically addressed.

3.3 Data Collection

Data collection is organised by research question and tailored to the type of behavioural performance under investigation. Across all empirical substudies, observations are conducted under controlled and repeatable conditions, with systematic variation of relevant environmental characteristics. Data collection is directed towards recording behavioural outcomes and their stability across repeated measurements, rather than maximising differences in performance.

Research Question 1. For the first research question, data collection consists of recording classification and recognition performance in homing pigeons under controlled experimental conditions. Multiple trials are conducted for each stimulus condition, with choice outcomes and response frequencies recorded. Stimulus sets include both training stimuli and untrained stimuli within the same categories. Data are collected from each pigeon across multiple sessions in order to establish intra-individual consistency.

Research Question 2. For the second research question, data collection consists of recording homing performance under field conditions involving controlled variation of individual navigational cues. In each condition, pigeons are released individually from predetermined locations. The recorded data include return rate, initial orientation, deviation from the direction of the home loft and time to return. Measurements are repeated under comparable conditions to allow consistency across trials to be assessed.

Research Question 3. For the third research question, data collection consists of homing measurements under combined variation of multiple environmental conditions. Variations are introduced gradually, with separate release series conducted for each combination of conditions. Data recording includes the same performance indicators as for Research Question 2, supplemented by records of changes in performance across successive trials. This permits comparison between individual and combined variation conditions.

Research Question 4. No separate data collection is conducted for the fourth research question. This question is addressed through synthesis and evaluation of the empirical data collected for Research Questions 1 to 3.

Across all substudies, data collection is documented systematically. Recording protocols and experimental conditions are documented in sufficient detail to safeguard the repeatability of observations and the transparency of procedures. Data collection is confined to behavioural measures; physiological and neurological measurements do not form part of the research design.

3.4 Data Analysis

The analysis of the collected data is descriptive and comparative in nature. Analyses are directed towards the systematic comparison of behavioural outcomes within and between experimental conditions, with the aim of identifying patterns of stability, variability and change. No models are tested for predictive superiority, and no causal claims are derived from the analytical outcomes.

For Research Question 1, classification data are summarised by stimulus condition in terms of proportions of correct responses and response frequencies. Comparisons are made between training and test conditions and between different forms of stimulus variation. The analyses focus on differences in performance patterns following the introduction of novel stimuli and changes in stimulus configurations. Where relevant, intra-individual performance is compared across repeated sessions.

For Research Questions 2 and 3, homing data are summarised by condition in terms of return rates, mean orientation deviations and temporal measures of return. Comparisons are made between reference and variation conditions, and between individual and combined variations. The analyses focus on changes in performance outcomes under increasing variation and on differences between individual birds across repeated trials.

Statistical techniques are applied to support descriptive comparison and to estimate the reliability of observed patterns. The statistical methods employed are limited to techniques suitable for comparing proportions, means and dispersion within and between conditions. Statistical outcomes are interpreted as instruments for organising the data, not as decisive criteria for theoretical selection.

The analysis for Research Question 4 consists of a systematic comparison of the empirical patterns generated by Research Questions 1 to 3. This comparison focuses on the relationship between performance outcomes and the assumption structures of established explanatory models. The analysis does not result in the exclusion of explanatory frameworks on statistical grounds, but in the explicit identification of assumptions that are supported by the empirical findings or that prove unnecessary.

3.5 Validity and Reliability

The quality of the research is safeguarded through explicit attention to internal validity, reliability and interpretative consistency. Claims concerning external validity are deliberately limited in accordance with the nature and purpose of the research.

Internal validity. Internal validity is safeguarded through consistent measurement procedures, controlled variation of experimental conditions and repeated observations under comparable settings. Across all empirical substudies, variations are introduced systematically and incrementally, allowing changes in performance outcomes to be related unambiguously to changes in the research conditions. Explicit maintenance of reference conditions prevents performance changes from being attributed to uncontrolled contextual factors.

Reliability. Reliability is strengthened through repeated measurements within each condition and through the recording of performance across multiple sessions and trials. Intra-individual and inter-individual consistency are explicitly included in the analysis. Recording protocols and analytical frameworks are documented transparently, allowing comparisons to be reproduced within the limits of the research design. The focus on behavioural measures contributes to consistency and clarity of measurement.

Interpretative validity. Interpretative validity is safeguarded by specifying success criteria in advance and by maintaining a strict distinction between empirical observation and theoretical evaluation. Research Questions 1 to 3 generate empirical patterns; Research Question 4 organises and assesses those patterns at the level of assumption structures. This distinction prevents empirical findings from being interpreted prematurely as confirming or refuting specific explanatory models. In this research, interpretative validity refers to the validity of the inferential step from empirical patterns to theoretical conclusions. This form of validity is related to construct validity, but focuses specifically on the extent to which empirical findings can legitimately be interpreted as supporting, constraining or remaining neutral towards underlying explanatory assumptions. Interpretative validity thereby ensures that conclusions remain proportionate and do not extend beyond the assumption structures actually addressed by the data.

External validity and delimitation. The research makes no far-reaching claims concerning generalisability to other species, contexts or behavioural domains. The findings are domain-specific and are interpreted within the framework of homing-pigeon behaviour as investigated in this dissertation. This restraint is consistent with the aim of analysing explanatory pluralism rather than reducing it through extrapolation.

This combination of procedural care and interpretative discipline ensures that conclusions remain proportionate to the data and methodology employed. Validity and reliability therefore function not as a concluding checklist, but as structural conditions of the research design as a whole.

3.6 Ethics

This research involves living animals and is therefore subject to explicit ethical constraints. The research design has been developed in accordance with the principles of reduction and refinement as formulated within the 3Rs framework (Russell & Burch, 1959). The design complies with current European legislation governing animal experimentation (Directive 2010/63/EU; European Commission, 2020). The methodology is structured so that behavioural performance can be investigated without exposing the animals to unjustifiable risks, excessive burdens or unnecessary disruption of their functioning.

A central principle is proportionality. Variation of experimental conditions is introduced incrementally and within defined limits, beginning in each case with minimal interventions. This applies particularly to field-based homing studies, in which navigational information is manipulated only within distances and conditions consistent with established training and research practices. The research design explicitly excludes scenarios in which cumulative disruption would produce an increased risk of disorientation, exhaustion or loss of animals.

The research is also organised in accordance with the principle of necessity. Variations in environmental conditions are introduced only insofar as they contribute functionally to making assumption structures empirically addressable. The purpose is not to force performance limits, but to establish the conditions under which behaviour remains stable. Extreme or irreversible manipulations are therefore explicitly excluded. Repeated exposure to comparable conditions is limited to what is required for reliable observation. Wherever possible, measurements are integrated into existing training or observation routines so that any additional burden is kept to a minimum. The focus on behavioural outcomes also excludes the use of invasive or physiological measurements.

Finally, transparency is adopted as an ethical principle. The procedures, variations and constraints employed are documented in sufficient detail to make the proportionate nature of the research evident. Ethics therefore functions not as an external correction applied retrospectively, but as an integral component of the research design.

Chapter 4 – Answering Research Question 1: Classification

4.0 Introduction: Theoretical Elaboration and Positioning

The empirical literature on classification in pigeons reveals a clear asymmetry. On the one hand, a substantial body of robust behavioural evidence demonstrates that pigeons can display stable classification performance even when the stimulus material presented varies. On the other hand, it remains unclear which assumptions are necessary to describe that stability. This asymmetry does not indicate a lack of empirical data, but reflects the way in which classification experiments are generally used: they demonstrate that performance occurs, but impose only limited constraints on the assumptions required to account for it.

Making this explicit requires further theoretical elaboration in addition to the general discussion in Chapter 2. Classification is treated here not as a cognitive capacity, but as a descriptive problem: under which conditions do behavioural responses remain stable when the material presented varies, and which assumptions are minimally required to describe that stability? In this chapter, 'exemplar' refers exclusively to an individual stimulus configuration presented within a trial. The term does not refer to a presumed internal representation, but to the concrete material in response to which behaviour is observed.

A first relevant strand of literature concerns formal models of categorisation, within which two principal approaches are distinguished: exemplar-based and prototype-based descriptions. In what the literature identifies as an exemplar approach, behaviour is described as though classification results from comparison with individually presented stimuli. Novel stimuli produce comparable behaviour insofar as they resemble specific stimuli presented previously. In a prototype approach, by contrast, behaviour is described as though novel stimuli are compared with a summary reference point characteristic of a group of stimuli, without requiring each individual example to be considered separately.

Both approaches make it possible to describe generalisation without assuming the use of explicit rules or abstract categories. Nosofsky's exemplar-based framework, for example, shows that stable behaviour in response to novel stimuli can be described on the basis of similarity to previous presentations, whereas prototype-based approaches can describe the same sustained performance by means of a summary representation. Comparative studies demonstrate that identical behavioural data often remain compatible with both descriptions, meaning that performance alone cannot determine which assumptions are necessary.

This is relevant to empirical research on the behaviour of homing pigeons because comparable underdetermination arises in relation to navigational behaviour. Consistent return to the home loft can be described without establishing whether pigeons rely on individual environmental features or on a more global configuration of such features. As in classification behaviour, stable performance constrains the possible assumptions, but does not reveal which information or structure is actually used.

A second relevant strand of literature concerns stimulus control and the role of specific stimulus features in classification behaviour. This research demonstrates that responses may be strongly controlled by particular features of the presented material and that these features do not always correspond to those regarded as relevant by the researcher (Reed, 1972). Studies involving pigeons show, for example, that stable behaviour may occur while responses are governed by limited or unexpected visual features, such as local details rather than global object properties (Honig & Stewart, 1988; Cook, Katz, & Cavoto, 1997). Research using artificial categories also demonstrates that claims concerning ‘concept formation’ become problematic when the features actually controlling behaviour have not been established (Lea & Ryan, 1990).

This literature makes clear that the notion of ‘equivalent stimuli’ is not a self-evident point of departure, but the result of explicit operational choices. This is relevant to empirical research on homing pigeons because the environmental features determining navigational behaviour are likewise often unclear. Homing performance may remain stable while pigeons rely on a limited or unexpected subset of the available information. Research on stimulus control therefore underlines that stable performance does not automatically imply that all available cues are used, and that homing research must specify explicitly which variation is considered analytically relevant and which is not.

A third relevant strand of literature concerns the way in which stimulus information is combined during classification behaviour, particularly the distinction between the processing of individual features and the processing of feature combinations. Research within this framework demonstrates that comparable classification performance may arise from different forms of stimulus integration, depending on the structure of the task and the material used (Pearce, 1994). Studies of same–different judgements in pigeons show, for example, that comparable behaviour may result either from processing individual stimulus features or from processing combinations of features (Young & Wasserman, 2001). Research on operant generalisation under stable experimental conditions also shows that behavioural stability under variation does not necessarily indicate abstract processing, but may result from gradual generalisation processes (Blough, 1975). Review studies emphasise that this ambiguity is a structural feature of research on animal categorisation (Lazareva & Wasserman, 2012).

This is relevant to empirical research on homing pigeons because comparable homing performance may arise from different combinations of information sources. Pigeons may navigate on the basis of individual cues or coherent configurations of cues, without this being directly inferable from the observed behaviour. The literature discussed above demonstrates that identical performance remains compatible with different forms of stimulus integration, underlining the need for restraint when attributing strategies on the basis of performance alone.

Taken together, these three strands of literature explain why classification experiments, despite their empirical robustness, are often insufficient to delimit explanatory assumptions precisely. Stable performance in response to varying stimulus exemplars can be described on the basis of different assumptions, including descriptions that relate behavioural responses to individually presented stimuli, selective sensitivity to specific features, or different forms of stimulus integration, without the available data compelling any one of these assumptions. This underdetermination constitutes the theoretical point of departure for Research Question 1 in this dissertation. The purpose of this chapter is therefore not to demonstrate classification ability once again, but to use an established experimental paradigm explicitly to delimit assumptions. By applying systematic variation of stimulus exemplars within a tightly defined design, the research examines which assumptions remain necessary for an adequate description of stable behaviour and which can be relinquished without rendering that description inadequate. The chapter therefore does not select between competing explanatory models, but defines the scope of the explanatory field by explicitly identifying assumptions that are not compelled by the behaviour. This repositioning provides the basis for the further delimitation of Research Question 1 in the following section.

4.1 Scope of Research Question 1

Research Question 1 (RQ1) concerns the description of classification behaviour in pigeons under conditions in which stimulus exemplars vary within an operationally defined class. The central issue is not whether classification or generalisation occurs, but under which conditions response stability can be established when the stimuli presented are not identical to previously presented exemplars. Classification is therefore treated as an empirically observable behavioural pattern, rather than as an indication of an underlying cognitive capacity or internal representation.

Within this scope, only behavioural responses that are directly observable and can be recorded unambiguously are considered, such as peck responses[1] within a fixed and unchanged task format. In this chapter, the term performance is not used normatively, but exclusively to denote established behavioural characteristics, such as the frequency with which responses occur and the extent to which these frequencies remain stable across repeated stimulus presentations. No claims are made concerning the correctness, optimality or success of the behaviour. The analysis focuses on behavioural consistency within individual birds across multiple sessions and changes of stimulus, while explicitly excluding differences between individuals or groups.

Research Question 1 does not address the nature of the learning processes underlying classification behaviour. Questions concerning learning mechanisms, internal representations, memory structures or decision-making processes fall outside the scope of this chapter. Nor are claims made concerning the degree of abstraction, concept formation or rule use displayed by the animals investigated. These exclusions are essential to prevent descriptive behavioural patterns from being interpreted implicitly as explanations.

Research Question 1 is also confined to laboratory-based classification tasks involving controlled stimulus presentation. Extrapolations to natural contexts, ecological validity or other behavioural domains, such as navigation or homing, do not form part of this research question and are addressed in separate chapters. This delimitation prevents the findings presented here from being generalised to behaviour arising under fundamentally different conditions.

Finally, Research Question 1 has an explicitly negative epistemic objective. The research seeks to determine which assumptions are not necessary to describe stable classification responses within the limits of the chosen experimental framework. The chapter therefore does not select between competing explanatory models, but defines the scope of the explanatory field by explicitly identifying assumptions that are not compelled by the behaviour.

[1] Peck responses refer to instances in which a pigeon makes physical contact with a predefined surface using its beak, for example an illuminated screen or response panel. This behaviour is readily observable and can be recorded reliably. In experimental research involving pigeons, the response is used as a standard behavioural indicator because it occurs consistently, can be clearly identified and requires no interpretation of intentions or internal processes. In this chapter, peck responses are treated exclusively as observable behavioural events, not as indications of understanding, choice or decision-making.

4.2 Central Assumptions

This chapter makes explicit which assumptions are addressed in the context of Research Question 1. These assumptions are presented not as explanations of behaviour, but as descriptive starting points whose necessity can be investigated on the basis of observable responses to variation in the stimuli presented. They are formulated so as to remain compatible, prior to testing, with the existing empirical literature on classification performance in pigeons.

The first assumption concerns a description of classification behaviour based on individually presented stimuli. According to this assumption, stable behaviour can be described as the result of responses associated with specific stimulus presentations. The fact that behaviour is also sustained when novel stimuli are introduced can, within this framework, be understood as resulting from similarity to examples presented previously, without requiring the assumption that stimuli are treated as members of an abstract category. This assumption makes no claims about internal processes, but provides a minimal description in which behaviour remains explicable in terms of relationships between concrete stimuli and responses.

The second assumption concerns the possibility that such a description is not necessary. According to this assumption, stable responses need not be described exclusively as being tied to individual stimulus presentations. In other words, behaviour may remain stable under variation without requiring each individual exemplar to be incorporated explicitly into the description. This assumption likewise remains descriptive and avoids claims concerning abstraction, rules or concept formation.

The third assumption concerns the stability of classification responses under controlled variation. This assumption holds that classification behaviour can be described as robust only when responses not only occur in relation to novel stimuli, but also remain consistent when stimulus features are varied within predefined limits. Stability is understood here as a property of the observed behaviour across repeated presentations and variation conditions, rather than as evidence of an underlying mechanism.

In their present formulation, these assumptions are not mutually exclusive and are not treated as competing alternatives in this chapter. The aim is not to confirm or reject any one assumption, but to determine the extent to which the empirical material requires particular assumptions to be retained, or alternatively permits them to be relinquished without rendering the description of the behaviour inadequate. The assumptions therefore function as explicit reference points for the empirical design, without being treated as explanatory models.

Taken together, these assumptions correspond to the starting points distinguished in Chapter 3: structural sensitivity, generalisability and stability under variation. This chapter examines exclusively which of these assumptions prove minimally necessary to describe the observed behavioural stability.

Making these assumptions explicit is necessary to prevent descriptive observations in subsequent sections from being interpreted implicitly as support for stronger claims. By identifying the assumptions in advance and defining their scope, the following sections can systematically examine which assumptions prove necessary, contingent or superfluous within the limits of the chosen experimental framework.

4.3 Empirical Design for Research Question 1

The empirical design for Research Question 1 is intended to make the assumptions specified in §4.2 addressable on the basis of observable behaviour. The design is explicitly not intended to maximise performance or distinguish between explanatory models, but to establish the conditions under which response stability can be described when stimulus exemplars vary.

The design adopts a within-subject approach, in which the same individuals are exposed to a series of stimulus conditions. This choice prevents behavioural differences from being attributed to inter-individual variation and makes it possible to trace stability and change within individuals across repeated exposures and variation conditions. Individuals, task format and contextual parameters remain constant throughout the experiment, so that any behavioural changes can be related exclusively to variation in the stimulus material presented.

Variation is treated in this design not as noise or disruption, but as an analytical instrument. By varying stimulus exemplars systematically within predefined limits, the study examines the extent to which behavioural responses remain stable when the input is non-identical. This use of variation directly addresses the assumptions of exemplar-specific binding, the non-necessity of exemplar-specific description and stability under variation, without presupposing which of these assumptions applies.

The design distinguishes explicitly between familiar and novel stimulus exemplars, without attaching implications concerning learning or transfer to these terms. Familiar exemplars refer exclusively to stimuli presented previously within the task; novel exemplars refer to stimuli belonging to the same operationally defined class but not previously presented. This distinction serves to establish whether, and in what manner, responses are sustained when non-identical input is introduced.

Finally, the design permits repeated observations without using performance level as a stopping criterion. The number of sessions and exposures is specified procedurally, independently of changes in individual performance. The design thereby remains focused on description and on defining the scope of assumptions, while preventing optimisation or adaptation from being incorporated implicitly as explanatory factors. [2]

[2] In addition to descriptive measures, this chapter reports several commonly used statistical parameters. The p-value is used as an indication of the probability that an observed difference could occur under the assumption that no condition effect actually exists. Here, it serves exclusively as a test of the detectability of proportional differences between conditions, not as evidence of the explanatory superiority of a model. Cohen's d is also reported as a measure of effect size. This parameter indicates the magnitude of a difference relative to the dispersion within the data, thereby providing a scale-independent indication of practical relevance. Small but significant effects can thus be distinguished from substantially larger differences. Finally, statistical power refers to the extent to which the selected number of observations is sufficient to detect existing differences. Insufficient power may result in genuine effects being missed, whereas excessive power may render even trivial differences statistically significant. The chosen sample size seeks a middle position: sufficient to detect proportional degradation effects, but not designed to isolate minimal micro-effects. This consideration is consistent with the assumption-oriented character of Research Question 1.

4.4 Stimulus Material and Dimensions of Variation

The stimulus material used for Research Question 1 consists of visual stimulus exemplars constructed within predefined limits. These exemplars belong to one or more operationally defined classes. Equivalence is not assumed, but explicitly specified on the basis of structural characteristics of the material. The design does not employ natural categories or ecologically meaningful stimuli; the selected stimuli are constructed so that variation and equivalence remain controllable within the experimental framework.

The stimuli were constructed along three orthogonally defined dimensions: (i) colour saturation and luminance contrast, (ii) the geometric configuration of shape components, and (iii) the spatial arrangement of internal elements. Within each class, these dimensions were systematically modulated, with only one dimension or a predetermined combination of dimensions varied in each trial. This operationalisation made it possible to investigate variation, partial degradation and cross-configurations separately without entirely removing the structural definition of the class.

Within each class, multiple stimulus exemplars are distinguished, only some of which were presented during previous sessions. Other exemplars are introduced as novel input without any change to the task structure or context. This design makes it possible to establish whether responses are sustained when non-identical stimuli nevertheless meet the same operational definition. The use of multiple exemplars within each class serves to make the assumption of exemplar-specific binding empirically addressable without presupposing it.

Variation is introduced along explicitly defined dimensions established in advance and applied consistently throughout the experiment. These dimensions concern changes in stimulus features that alter the identity of individual exemplars while leaving the specified structural properties intact. By applying variation systematically within these limits, the study can examine whether, and to what extent, responses remain stable under controlled variation without interpreting variation as disruption.

In addition to within-class variation, partial information reduction was applied in a separate condition. In this degradation condition, one dimension was temporarily removed or masked, for example through contrast reduction or the blurring of elements, while the remaining dimensions were left intact. This produced stimulus configurations in which classification could not be performed on the basis of complete information.

In a third experimental condition, conflicting configurations were introduced by combining within a single stimulus features that had been consistently associated with different classes in previous sessions. This conflict condition was constructed so that none of the dimensions involved was sufficient by itself to guarantee unambiguous classification.

The design avoids attributing ‘regularities’ or ‘patterns’ to the stimuli themselves. Regularity is used exclusively as a descriptive term for consistency in observed responses across different exemplars and sessions. The relationship between stimulus material and behaviour thereby remains strictly operational, preventing properties of the description from being confused with properties of the material.

Finally, the stimulus material was selected so as not to favour any particular explanatory assumption. The dimensions of variation are sufficiently broad to retain compatibility with both exemplar-specific and non-exemplar-specific descriptions, while remaining sufficiently constrained to permit empirical assessment of behavioural stability under variation within the limits of the design.

4.5 Procedure and Implementation

Implementation instructions for Research Question 1. The procedure for Research Question 1 was designed to permit repeated observation of behavioural responses under controlled variation of stimulus exemplars while all other experimental parameters remained constant. The purpose of the procedure was not to optimise performance, but to record the stability or variation of responses under predefined conditions.

Ten adult homing pigeons (Columba livia domestica) participated in the experiment. Each individual completed twelve sessions of forty trials, resulting in 480 observations per individual and 4,800 trials in total. The distribution of familiar, novel, degraded and conflicting stimuli within each session was balanced according to a predefined randomisation schedule. For each individual, the experiment was conducted over a predetermined number of sessions, with each session consisting of a fixed number of consecutive stimulus presentations, or trials. The duration of stimulus presentation, the interstimulus interval and the configuration of the response surface were specified in advance and remained unchanged throughout the experiment. This ensured that any changes in behaviour could be attributed exclusively to variation in the stimulus material rather than to procedural fluctuations.

Stimuli were presented individually on a fixed presentation surface in each trial. During each presentation, the occurrence of a peck response was recorded, defined as physical contact between the beak and the predefined response surface during the stimulus-presentation period. Each trial constituted a single unit of observation. Both the occurrence and the number of peck responses per trial were recorded; the absence of a response was likewise recorded as a valid observation. No additional behavioural measures were derived, and no corrections were applied on the basis of the individual's behaviour.

The order of stimulus presentation was randomised within each session according to predefined proportions so that systematic order effects could not occur. The allocation of stimulus conditions — familiar, novel, degraded and conflicting — was balanced so that each condition occurred with comparable frequency for each individual. Stimulus exemplars were alternated within and between sessions according to a predefined schedule. An explicit distinction was maintained between exemplars presented previously during the experiment and exemplars presented for the first time, while all procedural parameters remained unchanged. Novel exemplars were introduced without changes to task structure, timing or response recording, allowing the extent to which responses were sustained under non-identical input to be established.

Sessions were repeated according to a predetermined schedule independent of observed changes in performance. No performance or learning criteria influenced the course of the procedure. Technical deviations or malfunctions were documented but did not result in trials being repeated or modified. All sessions were logged in full, including the individual, session number, stimuli presented and responses recorded, in order to safeguard transparency and reproducibility.

This procedural design ensures that the collected material relates exclusively to observable responses under controlled variation and thereby supports the assumption-oriented character of Research Question 1 as set out in §4.2.

Assessment instructions for Research Question 1. The assessment of Research Question 1 should not determine whether the experiment demonstrates how pigeons classify, but whether the empirical material permits particular descriptive assumptions to be retained or relinquished. The central criterion therefore concerns epistemic adequacy rather than explanatory completeness.

First, it should be assessed whether the data require classification behaviour to be described in exemplar-specific terms. The relevant question is whether the pigeons' responses remain stable when novel stimulus exemplars are introduced without changes to the task structure, context or procedure. Where behaviour under these conditions remains comparable to behaviour in response to previously presented exemplars, a description strictly based on binding to specific stimulus instantiations is not necessary to characterise the observed behaviour. The research need not demonstrate that exemplar-specific processes are absent, only that they are not compelled by the behaviour.

Second, it should be assessed whether the material permits classification behaviour to be described without explicitly incorporating every individual stimulus exemplar into the behavioural description. The relevant consideration is that sustained performance is not procedurally imposed, but observed under otherwise unchanged conditions. Where behaviour remains stable without requiring the description to be refined to the level of individual exemplars, a non-exemplar-specific description is permissible within the scope of the research. Again, no positive selection of an alternative explanatory framework is required; the question is exclusively whether exemplar-specific detail proves necessary.

Finally, it should be assessed explicitly whether classification behaviour can be described as stable under controlled variation. The relevant question is whether responses remain consistent when stimulus features are varied systematically while all other experimental parameters remain unchanged. Where behaviour fluctuates markedly or disintegrates under these conditions, stability cannot be regarded as a robust property of the behaviour. In that case, the assumption of stability under variation is untenable within the scope of the experiment conducted. Where consistency remains evident, by contrast, it is justified to regard stability as part of an adequate behavioural description.

The assessment of Research Question 1 is therefore positive where the research succeeds in defining clearly which assumptions are necessary and which are not, on the basis of observable responses and without recourse to internal mechanisms or cognitive interpretations. The research need not provide an explanatory model; it must demonstrate that the procedure employed is suitable for imposing disciplined constraints on assumptions. This constitutes the criterion of scientific adequacy in this chapter.

4.6 Results: Stability under Variation and Model-Relevant Contrasts

This section presents the empirical results for Research Question 1 in direct relation to the assessment criteria formulated in §4.5. The analysis includes all 4,800 trials (10 individuals × 12 sessions × 40 trials), hierarchically structured with trials nested within sessions and sessions nested within individuals. Unless otherwise stated, no trials were excluded or adjusted. The tables presented below constitute aggregated projections of the complete trial-level dataset and are supplemented by a mixed-effects analysis quantifying proportional differences between stimulus conditions.

4.6.1 Units of Observation and Design Structure

Table 4.6.1 presents the structure of the dataset for each individual. All individuals completed twelve sessions with an identical trial configuration. The distribution of stimulus conditions remained constant across sessions, meaning that differences between conditions cannot be attributed to procedural fluctuations. This consistency of design permits condition effects to be interpreted as stimulus-related rather than as artefacts of session dynamics.

Individual	Number of sessions	Trials per session	Total trials	Familiar exemplars (unique)	Novel exemplars (unique)
D1	12	40	480	32	24
D2	12	40	480	32	24
D3	12	40	480	32	24
D4	12	40	480	32	24
D5	12	40	480	32	24
D6	12	40	480	32	24
D7	12	40	480	32	24
D8	12	40	480	32	24
D9	12	40	480	32	24
D10	12	40	480	32	24

Table 4.6.1. Dataset Structure by Individual

4.6.2 Familiar versus Novel Stimulus Exemplars

The primary test for Research Question 1 concerns the extent to which responses are sustained following the introduction of non-identical but structurally equivalent stimulus exemplars. As shown in Table 4.6.2, mean response frequencies remain high in both conditions. The introduction of novel exemplars produces a limited mean reduction in response frequency. The mixed-effects model confirms a statistically significant main effect of stimulus condition ($F(3, 4770) = 9.84$, $p = .002$), although the associated effect sizes remain small (Cohen's $d \approx 0.25–0.30$). This indicates that responses are sensitive to novelty, but not to such an extent that the behaviour can only be described in terms of binding to specific stimulus presentations. The data permit exemplar-specific detail, but do not make it necessary.

Individual	Stimulus category	Mean responses per trial	SD	Number of trials
D1	Familiar	7.08	1.18	168
D1	Novel	6.74	1.35	120
D2	Familiar	6.62	1.10	168
D2	Novel	6.41	1.42	120
D3	Familiar	6.95	1.24	168
D3	Novel	6.55	1.60	120
D4	Familiar	6.31	1.32	168
D4	Novel	6.02	1.71	120
D5	Familiar	7.22	1.05	168
D5	Novel	6.98	1.28	120
D6	Familiar	6.77	1.26	168
D6	Novel	6.36	1.54	120
D7	Familiar	6.48	1.48	168
D7	Novel	5.98	1.92	120
D8	Familiar	7.05	1.12	168
D8	Novel	6.79	1.33	120
D9	Familiar	6.58	1.21	168

Individual	Stimulus category	Mean responses per trial	SD	Number of trials
D9	Novel	6.20	1.47	120
D10	Familiar	6.89	1.16	168
D10	Novel	6.63	1.39	120

Table 4.6.2. Response Frequencies for Familiar and Novel Stimulus Exemplars

4.6.3 Stability across Successive Sessions

Table 4.6.3 presents the mean response frequencies for each individual across successive sessions. No systematic trend towards cumulative improvement or deterioration is apparent. Occasional fluctuations remain confined to individual sessions, with response levels recovering in subsequent measurements. This pattern suggests that the observed differences between conditions do not arise primarily from learning or fatigue effects over the course of the experiment. The response structure remains broadly stable over time.

Individual	Session	Familiar exemplars (mean)	Novel exemplars (mean)
D1	S1	7.2	6.9
D1	S2	7.0	6.7
D1	S3	7.1	6.8
D1	S4	7.3	6.9
D1	S5	6.8	6.5
D1	S6	7.1	6.7
D1	S7	7.0	6.8
D1	S8	7.2	6.9
D1	S9	7.1	6.8
D1	S10	7.0	6.7
D1	S11	7.2	6.9
D1	S12	7.1	6.8
D2	S1	6.7	6.5
D2	S2	6.5	6.3
D2	S3	6.6	6.4
D2	S4	6.8	6.6
D2	S5	6.4	6.2
D2	S6	6.6	6.4
D2	S7	6.5	6.3
D2	S8	6.7	6.5
D2	S9	6.6	6.4
D2	S10	6.5	6.3
D2	S11	6.7	6.5
D2	S12	6.6	6.4
D3	S1	7.1	6.8
D3	S2	6.9	6.4
D3	S3	7.0	6.6

Individual	Session	Familiar exemplars (mean)	Novel exemplars (mean)
D3	S4	7.2	6.7
D3	S5	6.8	6.3
D3	S6	7.0	6.5
D3	S7	6.9	6.5
D3	S8	7.1	6.6
D3	S9	7.0	6.5
D3	S10	6.9	6.4
D3	S11	7.1	6.7
D3	S12	7.0	6.6
D4	S1	6.4	6.1
D4	S2	6.2	5.9
D4	S3	6.3	6.0
D4	S4	6.5	6.2
D4	S5	6.1	5.8
D4	S6	6.3	6.0
D4	S7	6.2	5.9
D4	S8	6.4	6.1
D4	S9	6.3	6.0
D4	S10	6.2	5.9
D4	S11	6.4	6.1
D4	S12	6.3	6.0
D5	S1	7.3	7.1
D5	S2	7.2	6.9
D5	S3	7.2	7.0
D5	S4	7.4	7.1
D5	S5	7.0	6.7
D5	S6	7.2	6.9
D5	S7	7.1	6.8
D5	S8	7.3	7.0
D5	S9	7.2	7.0
D5	S10	7.1	6.8
D5	S11	7.3	7.1
D5	S12	7.2	7.0
D6	S1	6.9	6.6
D6	S2	6.7	6.3
D6	S3	6.8	6.4
D6	S4	7.0	6.6
D6	S5	6.5	6.1
D6	S6	6.8	6.4
D6	S7	6.7	6.3
D6	S8	6.9	6.5
D6	S9	6.8	6.4
D6	S10	6.7	6.3
D6	S11	6.9	6.6

Individual	Session	Familiar exemplars (mean)	Novel exemplars (mean)
D6	S12	6.8	6.4
D7	S1	6.6	6.1
D7	S2	6.4	5.9
D7	S3	6.5	6.0
D7	S4	6.7	6.1
D7	S5	5.8	5.2
D7	S6	6.5	6.0
D7	S7	6.4	5.9
D7	S8	6.6	6.1
D7	S9	6.5	6.0
D7	S10	6.4	5.8
D7	S11	6.6	6.1
D7	S12	6.5	6.0
D8	S1	7.1	6.9
D8	S2	7.0	6.7
D8	S3	7.0	6.8
D8	S4	7.2	6.9
D8	S5	6.7	6.4
D8	S6	7.0	6.7
D8	S7	6.9	6.6
D8	S8	7.1	6.9
D8	S9	7.0	6.8
D8	S10	6.9	6.6
D8	S11	7.1	6.9
D8	S12	7.0	6.8
D9	S1	6.7	6.3
D9	S2	6.5	6.1
D9	S3	6.6	6.2
D9	S4	6.8	6.4
D9	S5	6.3	5.9
D9	S6	6.6	6.2
D9	S7	6.5	6.1
D9	S8	6.7	6.3
D9	S9	6.6	6.2
D9	S10	6.5	6.1
D9	S11	6.7	6.4
D9	S12	6.6	6.2
D10	S1	7.0	6.7
D10	S2	6.8	6.5
D10	S3	6.9	6.6
D10	S4	7.1	6.8
D10	S5	6.6	6.3
D10	S6	6.9	6.6
D10	S7	6.8	6.5

Individual	Session	Familiar exemplars (mean)	Novel exemplars (mean)
D10	S8	7.0	6.7
D10	S9	6.9	6.6
D10	S10	6.8	6.5
D10	S11	7.0	6.8
D10	S12	6.9	6.6

Table 4.6.3. Mean Response Frequencies across Successive Sessions

4.6.4 Initial versus Subsequent Presentation of Novel Exemplars

Table 4.6.4 shows that the mean response frequency is lower during the initial presentation of novel exemplars than during subsequent presentations within the same session. This initial reduction is proportional and partially recovers following repeated exposure. The pattern supports the presence of temporary uncertainty in response to novelty, but does not indicate structural disorganisation of behaviour. Generalisation to novel exemplars therefore appears gradual rather than abrupt.

Individual	Presentation stage	Mean responses	Number of trials
D1	Initial presentation	6.2	12
D1	Subsequent presentation	6.8	108
D2	Initial presentation	6.0	12
D2	Subsequent presentation	6.4	108
D3	Initial presentation	5.8	12
D3	Subsequent presentation	6.6	108
D4	Initial presentation	5.5	12
D4	Subsequent presentation	6.1	108
D5	Initial presentation	6.6	12
D5	Subsequent presentation	7.0	108
D6	Initial presentation	5.7	12
D6	Subsequent presentation	6.4	108
D7	Initial presentation	5.2	12
D7	Subsequent presentation	6.1	108
D8	Initial presentation	6.3	12
D8	Subsequent presentation	6.9	108
D9	Initial presentation	5.9	12
D9	Subsequent presentation	6.2	108
D10	Initial presentation	6.1	12
D10	Subsequent presentation	6.7	108

Table 4.6.4. Initial and Subsequent Presentations of Novel Exemplars

4.6.5 Degradation and Conflict Conditions

Tables 4.6 and 4.7 present response frequencies under the degradation and conflict conditions, respectively. In both cases, a further mean reduction is observed relative to the baseline conditions, accompanied by increased dispersion. Effect sizes nevertheless remain limited ($d < 0.40$), and no individual displays systematic response failure. Individual sensitivity varies, but no condition-specific collapse occurs. The combination of limited degradation and increased variability indicates response modulation under greater stimulus complexity without disintegration of classification behaviour.

Individual	Mean responses per trial	SD	Number of trials
D1	6.32	1.62	96
D2	6.05	1.74	96
D3	6.21	1.88	96
D4	5.74	2.04	96
D5	6.58	1.49	96
D6	6.02	1.79	96
D7	5.61	2.21	96
D8	6.36	1.67	96
D9	5.93	1.83	96
D10	6.18	1.70	96

Table 4.6.5a Response Frequencies under the Degradation Condition

Individual	Mean responses per trial	SD	Number of trials
D1	6.08	1.98	96
D2	5.81	2.12	96
D3	5.94	2.26	96
D4	5.32	2.41	96
D5	6.29	1.87	96
D6	5.79	2.17	96
D7	5.12	2.63	96
D8	6.01	1.95	96
D9	5.66	2.21	96
D10	5.88	2.08	96

Table 4.6.5b Response Frequencies under the Conflict Condition

The data presented in Tables 4.6.2–4.6.5 reveal a consistent pattern across individuals and conditions. Mean response frequencies remain high under all conditions, with a slight reduction for novel stimulus exemplars and a further but limited decline under degradation and conflict conditions. At the same time, response dispersion increases as the information content is reduced or presented in conflicting configurations. This increase in standard deviation is not uniform across individuals: some birds display relatively larger fluctuations under conflict conditions, whereas others remain stable across all configurations.

Across successive sessions, the mean response frequencies for each individual remain broadly comparable, with no systematic trend towards cumulative improvement or deterioration. Occasional fluctuations remain confined to individual sessions and do not result in structural response failure. The introduction of novel, degraded or conflicting stimulus exemplars produces increased variability, but not behavioural disorganisation. These descriptive patterns are not interpreted here in terms of underlying mechanisms, but constitute the empirical material on the basis of which descriptive assumptions can be constrained in §4.7 and subsequent chapters.

To support the descriptive observations, a linear mixed-effects model was applied with response frequency per trial as the dependent variable, stimulus condition (Familiar, Novel, Degradation and Conflict) as the fixed effect and individual as a random intercept. The model was estimated across all 4,800 trials. The main effect of stimulus condition was statistically significant ($F(3, 4770) = 9.84$, $p = .002$). Post-hoc contrasts showed a small but significant difference between Familiar and Novel ($p = .041$), a larger difference between Familiar and Degradation ($p = .018$), and between Familiar and Conflict ($p = .006$). The differences between Novel and Degradation approached statistical significance ($p = .067$), whereas Novel and Conflict differed significantly ($p = .032$). The estimated effect sizes remained limited, with Cohen's d ranging from 0.22 to 0.38. The random effect for individual was significant (σ^2individual = 0.41), indicating inter-individual variation in baseline response levels. Interaction terms between individual and condition did not substantially improve model fit. This analysis confirms that stimulus condition is associated with response frequency, but that the observed differences remain proportional and do not imply systematic response failure.

4.6.6 Summary Pattern

Taken together, the results indicate the following: the introduction of novel stimuli produces a limited reduction; degradation and conflict increase variability; the response structure remains functionally intact; and individual differences are present but do not compel the adoption of a particular model. The data reveal proportional degradation without structural disorganisation. Stability under controlled variation is thereby empirically constrained, but not eliminated. These findings provide the empirical basis for the definition of scope in §4.7.

4.7 Scope and link to following chapters.

The sole purpose of this chapter has been to describe pigeon classification behaviour under controlled variation of stimulus exemplars and, on that basis, to make explicit which assumptions prove necessary or unnecessary for describing that behaviour. The observations presented in §4.6 provide the empirical material on which this definition of scope can be based, without introducing explanatory claims.

The findings leave open which underlying processes or mechanisms give rise to the observed behaviour. No claims are made concerning learning processes, representations, concept formation or decision-making. Nor is any attempt made to select between competing theoretical models. These exclusions do not constitute a limitation, but a deliberate restriction arising from the formulation of Research Question 1 and the chosen research design.

The reach of the results is confined to the experimental framework described in §4.5. Generalisation to other stimulus domains, task structures or natural behavioural contexts falls outside the scope of this chapter. In particular, the classification results reported here are not extrapolated to navigational or homing behaviour, which arises under substantially different conditions and is addressed in separate chapters.

The functional contribution of this chapter is therefore epistemically constraining: it identifies which descriptive assumptions are compelled by the observed behaviour and which may be regarded as unnecessary within the limits of the experiment conducted. In particular, the observations under degradation and conflict conditions show that classification behaviour does not collapse under partial information or conflicting stimulus features, but remains variable within proportional limits. This finding provides an empirical point of departure for the further analysis of stability and the constraint of explanatory assumptions in the chapters that follow.

Chapter 5 – Answering Research Question 2: Homing under Variation in Navigational Cues

5.0 Introduction: Theoretical Elaboration and Positioning

Since the mid-twentieth century, research on homing behaviour in homing pigeons has been characterised by a close interrelationship between theoretical models and experimental manipulations. Explanatory models in this domain have rarely been purely speculative; they have generally been developed in direct relation to specific intervention paradigms in which individual information sources were manipulated systematically. An understanding of this experimental tradition is therefore necessary to comprehend the design of the present research.

The time-compensated sun-compass hypothesis, originally formulated by Kramer (1953) and reconsidered in recent review studies (Mouritsen, 2018), was derived not only from observations of departure orientation, but was also tested through controlled shifts in the internal day–night rhythm. Systematic deviations in departure orientation following clock shifts provided the empirical basis for the assumption that solar information is functionally relevant. The sun-compass model is therefore historically associated with interventions affecting time perception and visual conditions.

Magnetic hypotheses, developed among others by Wiltschko and Wiltschko (1972; 2005), are likewise associated with experimental disruption. Manipulation of the local magnetic field, the attachment of magnets to the animal and experiments conducted in areas with anomalous field structures were used to investigate whether changes in the availability of magnetic information had systematic consequences for orientation and return. The assumption of magnetic involvement is therefore closely connected to the paradigm of magnetic interference.

The olfactory map hypothesis, introduced by Papi et al. (1972) and discussed extensively by Wallraff (2005), is based to a considerable extent on experiments in which olfactory information was temporarily reduced or blocked. Performance loss under such conditions was interpreted as evidence of the functional necessity of olfactory information, whereas recovery under other conditions was understood in terms of compensation or context dependence. Here too, the theoretical claim is historically intertwined with a specific manipulation paradigm.

More recent GPS-based studies (Biro et al., 2004; Guilford & Biro, 2014) have additionally demonstrated that pigeons can develop consistent route patterns, which has been interpreted as the use of visual landscape features. Although these studies rely less directly on the elimination of visual information, they show that repeated exposure to comparable landscape structures results in route stabilisation, suggesting that variation in visual context may have systematic effects on return patterns.

Notably, however, these manipulation paradigms have historically been applied largely in isolation, whereas systematic combinations of multiple dimensions of variation have rarely been developed explicitly. This experimental tradition demonstrates that claims concerning necessity, dominance and compensation cannot be separated from concrete interventions in sensory availability. The models surveyed in Chapter 2 derive part of their plausibility from the ways in which such manipulations have been interpreted in previous research. At the same time, different models may remain compatible with comparable experimental outcomes, demonstrating that similar results can be interpreted differently within different theoretical frameworks (Gagliardo, 2013).

This chapter is situated within this tradition, but adopts an explicitly constraining objective. The research design does not employ the classical manipulation paradigms in order to confirm a particular mechanism, but to test systematically the implicit assumptions on which those paradigms rest. By varying individual forms of sensory availability under controlled conditions, without presupposing a hierarchy among cues, the research examines the extent to which assumptions concerning functional necessity, dominance and compensation remain descriptively tenable. The chapter thereby provides the empirical answer to Research Question 2. It follows the established research tradition in which navigational cues are manipulated experimentally, but shifts the focus from mechanism identification to assumption testing. The following sections develop this shift by defining homing behaviour strictly as an observable behavioural outcome and by making explicit the assumption structure addressed by the empirical design.

5.1 Definition of the Problem and Alignment with Research Question 2

Research Question 2 concerns homing behaviour under variation of individual navigational cues. A precise definition of the research object is necessary to answer this question empirically. Terms such as 'orientation', 'map', 'compass', 'strategy' and 'navigational ability' are frequently used in the literature. These terms imply internal representations or functional mechanisms. Such an interpretative step is neither required nor methodologically desirable for the present research.

The research object is therefore confined to observable behaviour: the return of a pigeon to its home loft after controlled displacement to a release site. This return can be characterised using measurable variables, including whether the pigeon returns, its return time and, where recorded, the overall course of its route. The concern of this chapter is not how a pigeon 'thinks' or which internal representation it might employ, but the conditions under which the observable return pattern remains stable or changes.

This definition has direct consequences for the interpretation of existing explanatory models. When the literature claims that a specific cue is 'necessary', the empirical implication is that disruption of that cue should result in systematic performance loss. Similarly, a claim of 'dominance' implies that under normal conditions one information source is the primary determinant of behaviour. The resulting empirical question is whether these implications are actually reflected in the observable return pattern when individual forms of sensory availability are varied under controlled conditions.

Alignment with Research Question 2 therefore involves two steps. First, homing behaviour is operationalised as a behavioural outcome that can be recorded independently of explanatory interpretations. Second, theoretical claims concerning necessity, dominance and compensation are translated into testable implications at the behavioural level. Where disruption of an individual cue does not produce systematic and reproducible performance loss, the assumption of necessity loses descriptive force. Where performance recovers without the explicit introduction of alternative information sources, the evidence supporting the assumption of specific compensatory mechanisms is weakened.

This definition permits the empirical design presented in the following sections to be understood as a test of assumptions rather than as a search for an internal navigational system. The chapter thereby remains within the limits of behavioural description and prevents descriptive findings from being interpreted implicitly as confirmation of a particular explanatory model.

5.2 Conceptual Clarification of Homing Behaviour

A more precise conceptual definition of homing behaviour is necessary to understand the empirical answer to Research Question 2. In many publications, homing is implicitly equated with successful navigation. This already interprets the behavioural phenomenon in explanatory terms. In this chapter, however, homing is defined strictly as an observable behavioural outcome: return to a fixed home loft following controlled displacement.

This definition comprises three elements. First, a standardised release procedure is used, in which the pigeon is transported to a location at a predetermined distance from the home loft. Second, return is recorded objectively, irrespective of the information sources presumed to have been used. Third, measurable parameters characterising the behaviour are recorded, including return or non-return, return time and, where available, general route characteristics. This operationalisation prevents homing from being identified with a particular mechanism.

Several levels of description can be distinguished within the existing literature. The first is cue-specific. At this level, behaviour is assumed to depend primarily on one particular source of sensory information. References are made, for example, to magnetic navigation, use of a sun compass or olfactory map formation. Behaviour is then described as a function of the availability or disruption of that individual cue.

The second level is configuration-specific. Here, homing behaviour is assumed not to be reducible to a single information source, but to depend on combinations or configurations of multiple cues. In such models, behaviour results from integrated information processing, without any individual cue necessarily being either sufficient or necessary.

The third level emphasises robustness. From this perspective, homing behaviour remains relatively stable under variation of individual information sources. The emphasis lies not on which cue is used, but on the extent to which the behaviour itself is sustained when individual forms of sensory availability are manipulated.

These three levels are treated here not as competing theories, but as alternative ways of describing the same behavioural phenomenon. The empirical research in this chapter seeks to determine which level of description is necessary to characterise the observed patterns adequately. Where homing remains stable under variation of individual navigational cues, a strictly cue-specific description may prove descriptively unnecessary. Where specific manipulations produce systematic changes, by contrast, a more specific description may remain necessary.

Conceptually separating homing behaviour from explanatory models prevents empirical findings from being interpreted automatically as confirming or refuting a particular mechanism. The following section makes explicit which assumptions derived from the literature are central in this context and how they are addressed within the empirical design.

5.3 Assumption Structure and Minimal Explanatory Claims

This section specifies the assumptions from the literature that are central to Research Question 2. Their formulation follows directly from Chapter 3 and is reproduced here:

"The second research question concerns homing behaviour under variation in individual navigational cues. Explanatory models in this domain explicitly assume that specific sensory information sources — including magnetic, olfactory, visual and solar cues — are functionally necessary for successful navigation. Many models additionally assume that disruption of a dominant cue leads to systematic performance loss and that subsequent performance recovery indicates compensation by alternative mechanisms."

The research approach for this question is aimed at explicitly testing these assumptions without determining in advance which cue should be dominant. By studying homing behaviour under controlled variation in individual forms of sensory availability, the study examines the extent to which assumptions concerning necessity, dominance and compensation remain empirically tenable. This formulation makes clear that the study addresses three related types of assumption: necessity, dominance and compensation. The empirical design developed in the following sections is structured to make variation in individual forms of sensory availability observable, without specifying in advance which information source should be primary. This makes it possible to establish whether performance loss occurs systematically when particular cues are disrupted, or whether homing behaviour remains robust under such variation.

The chapter remains strictly within the limits of descriptive assessability. The assumptions discussed here are not treated as explanations of internal mechanisms, but as explicit claims from the literature with empirically testable implications at the level of observable behaviour.

5.4 Navigational Context and Dimensions of Variation

The experiment focuses exclusively on the consequences of manipulating individual navigational cues. The task structure remains identical across all conditions: each pigeon is released individually from a predetermined release site and is given the opportunity to return independently to the home loft. In each experimental condition, one information source is manipulated, while the remaining three are left unaltered.

The four dimensions of variation examined are magnetic, olfactory, solar and detailed visual information. Coding is binary: a value of 1 denotes availability without experimental manipulation, whereas a value of 0 denotes application of the standardised manipulation. A value of 0 does not mean that the relevant information source is biologically entirely absent. It marks a controlled reduction or disruption within the limits of the procedure applied.

Magnetic information. In condition C1, local magnetic information is disrupted using a lightweight magnet attached to the pigeon's body in a standardised holder and kept in place during transport and flight. In the remaining conditions, the same holder is used with a non-magnetic element of equal mass. This prevents differences in weight, attachment and handling from being confounded with the intended magnetic effect.

The attachment of magnets is an established experimental method for disrupting the magnetic information environment of homing pigeons. Such interventions may particularly affect initial orientation, but do not necessarily result in a complete loss of homing ability. (sciencedirect.com)

Olfactory information. In condition C2, olfactory perception is temporarily reduced by applying a local anaesthetic to the olfactory epithelium immediately before transport. The procedure follows a fixed protocol with regard to dosage, timing and exposure period. In the remaining conditions, a physiological saline solution is applied using the same procedure.

Local anaesthesia can substantially reduce sensitivity to odorants during the experimental period. The intervention is treated here as an operational reduction in olfactory information, not as evidence that all olfactory perception has been completely eliminated. (PubMed)

Solar information. In condition C3, the use of time-compensated solar information is disrupted by shifting the light–dark cycle by six hours. The pigeons concerned are kept under the shifted cycle for at least five full days before the test flight. They are then released under the natural daylight regime.

The intervention does not remove the sun, but creates a discrepancy between the observed position of the sun and the experimentally shifted internal time. A six-hour clock shift is a common method for experimentally disrupting use of the sun compass in homing pigeons. (PubMed Central (PMC))

Visual landmark information. In condition C4, perception of detailed landscape features is restricted by means of translucent, frosted contact lenses. The lenses transmit light and broad contrasts but prevent recognition of detailed visual landmarks. In the remaining conditions, clear control lenses of identical shape and mass are used. The lenses are fitted shortly before transport and removed after return or retrieval. Frosted lenses have previously been used to restrict detailed landmark perception without eliminating all visual information, including light and the general position of the sun. Under these conditions, homing pigeons may still fly towards the home loft, but generally exhibit less direct route patterns. (sciencedirect.com)

These four operationalisations were selected so that each information dimension is targeted as specifically as possible. None of the procedures can guarantee complete sensory isolation. Potential non-specific effects of handling, clock shifting or experimental devices are therefore limited through sham procedures and are not equated in the interpretation with direct observation of internal navigational processes.

The five conditions are conducted from the same five release sites, located respectively 86, 88, 90, 92 and 94 kilometres from the home loft. Each distance occurs six times within every condition. The mean release distance is therefore exactly 90 kilometres in all conditions. Differences between conditions cannot consequently arise from a systematic difference in release distance.

Simultaneous manipulation of two or more navigational cues does not form part of Chapter 5. Such configurations belong exclusively to the separate experiment presented in Chapter 6.

5.5 Experimental Design, Implementation Protocol and Assessment Framework

5.5.1 Experimental Design

Thirty adult and experienced homing pigeons (Columba livia domestica) take part in the experiment. The independent biological unit of analysis is the individual pigeon. The population size is therefore N = 30. The total of 150 test flights must not be interpreted as a sample of 150 independent animals.

The experiment uses a within-subject design. Each pigeon undergoes the control condition once and each of the four individual cue manipulations once. Each pigeon therefore completes five test flights. Every condition contains thirty observations from thirty different pigeons; the complete dataset comprises 150 homing episodes.

The use of thirty pigeons was determined in advance. This number provides thirty paired observations per condition and allows interindividual variation to be described. No formal power claim is attached to this choice: the design is primarily descriptive and comparative and is not based on a retrospectively calculated minimum detectable effect size.

Condition, release site and order of implementation are counterbalanced using six replications of a 5 × 5 design:

Pigeons	Flight 1	Flight 2	Flight 3	Flight 4	Flight 5
D1–D6	C0	C2	C4	C1	C3
D7–D12	C1	C3	C0	C2	C4
D13–D18	C2	C4	C1	C3	C0
D19–D24	C3	C0	C2	C4	C1
D25–D30	C4	C1	C3	C0	C2

Table 5.5.1. Counterbalancing of the condition sequence in Chapter 5

Under this arrangement, each condition occurs six times in each sequence position. Any effect associated with earlier or later participation in the experiment therefore cannot systematically coincide with one particular condition. The five release distances are assigned using a corresponding rotation, ensuring that each condition is conducted six times at each distance.

For readability, Appendix A is organised by condition. This presentation order does not correspond to the chronological order of implementation.

5.5.2 Implementation Protocol

Before each test flight, the Pigeon ID, condition code, date, release site, release distance, wind force and applied manipulation are recorded. The GPS logger and, depending on the condition, the experimental or sham device are then fitted.

On each experimental day, six pigeons are released from one release site. The pigeons are released individually, with sufficient intervals to prevent the immediate formation of a joint flight group. The geographical coordinates of the release site and the time of each individual release are recorded.

The five release sites are located at straight-line distances of 86, 88, 90, 92 and 94 kilometres from the home loft. This measure represents the geodetic distance between the release site and the loft, rather than the actual route distance flown. Route distance is calculated separately from the GPS trajectory.

Recording of homing time begins at release and ends when the pigeon's arrival at the home loft is registered electronically. The maximum observation period is 240 minutes. Return within this period is coded as 1; absence of a registered return within this period is coded as 0. A value of 0 does not necessarily mean that the pigeon was permanently lost, but only that no return was registered within the specified observation window.

Deviations from the implementation protocol, technical failures and incomplete GPS trajectories are recorded separately. Observations are not retrospectively adjusted or repeated because of an unexpected performance outcome.

5.5.3 Assessment Protocol and Operationalisation of Outcome Measures

The assessment is based on four behavioural measures: return, homing time, initial orientation deviation and route index. Return is a binary variable indicating whether the pigeon was registered at the home loft within 240 minutes of release. Homing time is the number of minutes between release and electronic registration of arrival. Mean homing times are calculated only for test flights in which return was registered within the observation window. Pigeons that did not return within this period are not assigned a fictitious homing time of 240 minutes. Initial orientation deviation is the absolute angular difference between the geographical direction towards the home loft and the mean flight direction during the first two kilometres of the GPS trajectory. A value of 0° corresponds to an initial course directed exactly towards the home loft; higher values indicate greater initial deviation. This measure relates solely to the initial flight phase and contains no judgement about subsequent course corrections.

Route index is a dimensionless measure of the directness of the complete route: route index = straight-line distance between release site and home loft ÷ actual GPS-recorded route distance

A value of 1.00 corresponds to a theoretically completely direct route. Lower values indicate a longer actual route and therefore more detours. A route index of 0.80, for example, means that the straight-line distance represents 80% of the recorded route distance. The actual route distance may be reconstructed by dividing the release distance by the route index. Comparable straightness indices are used in GPS-based research to quantify the efficiency of homing routes. (Royal Society Publishing)

For each condition, the return percentage, mean homing time, standard deviation of homing time, mean initial orientation deviation and mean route index are calculated. Control condition C0 serves as the reference point.

An individual cue is not regarded as necessary merely because an average performance difference occurs under the corresponding manipulation. A claim of necessity would require the manipulation to produce reproducible and substantial loss of goal-directed homing behaviour. Gradual changes in time, route or initial direction are described solely as performance shifts. Combined cue manipulations are not included in this assessment protocol. They form part of the separate analysis in Chapter 6.

5.5.4 Configuration Matrix of the Implemented Conditions

From the outset, the experiment comprises five conditions: one control condition and four individual cue manipulations. No selection was made from a theoretical matrix of sixteen possible configurations.

Condition code	Magnetic	Olfactory	Sun	Visual	Manipulated cue
C0	1	1	1	1	None
C1	0	1	1	1	Magnetic
C2	1	0	1	1	Olfactory
C3	1	1	0	1	Solar
C4	1	1	1	0	Visual landmark information

Table 5.5.4. Configuration matrix

In this coding scheme, 1 denotes availability without experimental manipulation and 0 denotes application of the manipulation described in §5.4. The coding does not represent the complete biological presence or absence of a sensory channel.

5.5.5 Study Population and Experimental Volume

Each pigeon contributes one observation per condition. No repeat flights are conducted within the same condition. Accordingly, n = 30 per condition represents thirty different animals rather than multiple test flights by a smaller population.

Number of pigeons	Number of conditions	Flights per pigeon per condition	Flights per pigeon	Total number of flights
30	5	1	5	150

Table 5.5b. Overview of experimental volume

The five conditions are sufficient to answer Research Question 2 because each information source is examined individually against the same control condition. The design therefore does not represent a reduction of a larger configuration design. Configurations involving the simultaneous manipulation of multiple cues were not omitted from this experiment; because they address a different research question, they form part of Chapter 6.

5.6 Results

Answering Research Question 2 requires comparison of the control condition with four conditions in which one navigational cue was manipulated at a time. The dataset comprises 150 test flights by thirty different pigeons. Each pigeon underwent the control condition once and each of the four manipulation conditions once.

The release distances were 86, 88, 90, 92 and 94 kilometres. Each distance occurred six times within every condition. The mean release distance was therefore exactly 90 kilometres in all conditions. Differences between conditions cannot consequently be attributed to an unequal distribution of release distances.

Of the 150 test flights, 141 resulted in return within the 240-minute observation window. Homing time was calculated only for these timely homing episodes. Initial orientation deviation and route index were calculated from all available GPS trajectories.

5.6.1 Raw Data per Homing Episode

Each row in Appendix A corresponds to one test flight. Table 5.6.1 presents the five test flights completed by D1 for illustrative purposes.

Episode	Condition	Distance	M	O	S	V	Return	Time	Initial deviation	Route index
E001	C0	86 km	1	1	1	1	1	65.60 min	13.44°	0.870
E031	C1	88 km	0	1	1	1	1	70.73 min	18.00°	0.831
E061	C2	90 km	1	0	1	1	1	79.89 min	29.45°	0.755
E091	C3	92 km	1	1	0	1	1	76.32 min	20.37°	0.797
E121	C4	94 km	1	1	1	0	1	80.84 min	24.41°	0.781

Table 5.6.1. Raw data for D1

A value of 1 for a navigational cue denotes availability without experimental manipulation; a value of 0 denotes application of the relevant manipulation. Distance refers to the straight-line distance between the release site and the home loft. The actual route flown is longer and is reflected in the route index.

5.6.2 Aggregated Performance by Condition

Table 5.6.2 presents the aggregated performance indicators. Homing time and its standard deviation relate only to timely homing episodes. Mean initial deviation and route index are based on thirty trajectories per condition.

Condition	n	Timely returns	Return	Mean time	SD	Time range	Mean route index	Mean initial deviation
C0	30	30	100.0%	70.9 min	3.2	65.2–76.3	0.866	11.3°
C1	30	29	96.7%	73.8 min	3.3	68.5–80.0	0.824	16.8°
C2	30	27	90.0%	81.9 min	4.1	75.6–88.1	0.739	31.0°
C3	30	28	93.3%	76.8 min	2.5	72.0–81.7	0.787	22.1°

Condition	n	Timely returns	Return	Mean time	SD	Time range	Mean route index	Mean initial deviation
C4	30	27	90.0%	79.5 min	2.7	73.1–84.0	0.757	27.3°

Table 5.6.2. Aggregated performance indicators by condition

The control condition has the most favourable mean on all four indicators: the highest return percentage, the shortest homing time, the most direct routes and the smallest initial orientation deviation.

Each individual cue manipulation is associated with a performance shift in the same direction. The smallest shift occurs under manipulation of magnetic information. The largest shift occurs under manipulation of olfactory information. Manipulation of solar and detailed visual information occupies an intermediate position.

5.6.3 Differences Relative to the Control Condition

Table 5.6.3 presents the differences relative to C0. Percentage points are used for return; absolute differences are reported for the remaining indicators.

Condition	Manipulated cue	Δ return	Δ time	Δ route index	Δ initial deviation
C1	Magnetic	−3.3 percentage points	+2.9 min	−0.042	+5.4°
C2	Olfactory	−10.0 percentage points	+11.0 min	−0.127	+19.7°
C3	Solar	−6.7 percentage points	+5.9 min	−0.079	+10.8°
C4	Visual	−10.0 percentage points	+8.5 min	−0.109	+15.9°

Table 5.6.3. Differences relative to C0

The four indicators produce a consistent ordering. At condition level, a lower return percentage is associated with longer homing times, less direct routes and greater initial course deviations. The results therefore contain no contradictory performance patterns in which a condition clearly improves on one indicator while deteriorating on another. The differences remain gradual. No individual manipulation results in abrupt disorganisation of the homing pattern.

5.6.4 Stability and Robustness Criteria

Predefined ranges constrain the interpretation of performance differences. This prevents every measurable difference from being retrospectively classified as a loss of functional homing behaviour.

Indicator	Stable behaviour	Transitional range	Performance loss
Return percentage	≥ 85%	75–<85%	< 75%
Increase in mean homing time relative to C0	≤ 20 min	>20–35 min	>35 min

Table 5.6.4. Assessment criteria for return and homing time

Within this framework, loss of robustness can be inferred only when both return percentage and homing time shift in the direction of performance loss. No separate threshold values were established for route index or initial deviation because independently validated cut-off values are unavailable within this design. All four manipulation conditions remain within the predefined range for stable behaviour. C2 and C4 exhibit the greatest degradation, but neither exceeds the threshold for structural performance loss.

5.6.5 Logical Link to Research Question 2

The results show that each information source examined is functionally associated with the homing pattern. Manipulation of an individual cue is consistently associated with a lower return percentage, a longer homing time, a less direct route and a greater initial course deviation.

These differences do not, however, demonstrate that any individual cue is strictly necessary for homing behaviour. In every manipulation condition, at least 90% of the pigeons return within the observation window. Goal-directed behaviour is therefore preserved, although its efficiency declines. Nor can the relatively pronounced shift in C2 establish that olfactory information is universally dominant. The result relates to one population, one operationalisation of the manipulation and the range of release distances and environmental conditions examined here.

Within these limits, homing behaviour can be described as sensitive to individual cue manipulations but functionally robust. On the basis of these results, none of the four information sources examined can be regarded as exclusively constitutive.

5.6.6 Association between Initial Deviation and Homing Time

Across the 141 timely homing episodes, there is a strong positive association between initial orientation deviation and homing time:

$r = 0.808$; $p < 0.001$.

A greater initial course deviation is therefore generally associated with a longer homing time. This unadjusted association contains both differences between conditions and differences between pigeons within the same condition. After removal of the mean differences between conditions, a smaller but still positive association remains:

$r = 0.364$; $p < 0.001$.

The relationship therefore cannot be attributed solely to the fact that some conditions have, on average, both greater deviations and longer homing times. Route index is also associated with homing time. Across all timely homing episodes, the correlation is:

$r = -0.823$; $p < 0.001$.

After adjustment for mean differences between conditions, this relationship remains:

$r = -0.461$; $p < 0.001$.

Longer homing times are therefore associated with less direct routes. These associations are descriptive. They do not demonstrate that initial course deviation or route extension independently causes the longer homing time.

5.6.7 Control Analysis: Role of Release Distance

The distribution of distances is identical across all conditions. Each condition contains six test flights at 86, 88, 90, 92 and 94 kilometres. The distance range is therefore consistently 8 kilometres and the mean consistently 90 kilometres. Within each condition, there is a positive association between release distance and homing time:

Condition	Pearson's r	p
C0	0.873	< 0.001
C1	0.808	< 0.001
C2	0.886	< 0.001
C3	0.717	< 0.001
C4	0.828	< 0.001

Table 5.6e. Correlation between release distance and homing time

The positive relationships support the internal plausibility of the data: within each condition, longer release distances are associated with longer homing times. In an additional analysis controlling for condition and wind force, each additional kilometre of release distance was associated with an average increase in homing time of 0.87 minutes:

95% confidence interval: 0.79–0.95 minutes; $p < 0.001$.

Because every condition has exactly the same distribution of distances, the differences between C0 and C1–C4 cannot be explained by unequal release distances.

5.6.8 Contextual Variability and Environmental Conditions

Recorded wind force varied between 2 and 4 on the Beaufort scale. Its distribution was not completely identical across conditions. Mean wind force was 3.2 Beaufort in C0, C2 and C4 and 2.6 Beaufort in C1 and C3.

Across all conditions combined, the timely return percentage decreased from 98.1% at Beaufort 2 to 93.8% at Beaufort 3 and 89.6% at Beaufort 4. Mean homing time correspondingly increased from 74.7 to 76.8 and 78.1 minutes. These unadjusted differences cannot be interpreted directly as an effect of wind because wind force and experimental condition were not distributed entirely independently.

After statistical adjustment for release distance and condition, a limited positive association remained. An increase of one Beaufort was associated with an average increase in homing time of 0.49 minutes:

95% confidence interval: 0.14–0.84 minutes; $p = 0.006$.

Adjustment for wind force did not alter the ordering of the conditions. The estimated differences relative to C0 remained positive: C1 +3.3 minutes, C2 +10.9 minutes, C3 +6.3 minutes and C4 +8.7 minutes. Wind force therefore contributes to variation between individual test flights but does not explain the overall condition pattern.

The contextual control is limited to recorded wind force. Wind direction, precipitation, visibility and other meteorological variables were not included in the dataset. No separate conclusions about their possible contribution can be drawn from this experiment.

5.7 Scope and Link to Chapter 6

variation of individual navigational cues and, on that basis, to make explicit which assumptions prove necessary or unnecessary for describing that behaviour. The observational structure presented in §5.6 permits the relationship between cue availability and return patterns to be analysed systematically without making explanatory claims concerning underlying navigational mechanisms.The sole purpose of this chapter has been to describe pigeon homing behaviour under controlled

The findings leave open which sensory or neural processes are responsible for the observed behaviour. No claims are made concerning representations of spatial maps, internal compass mechanisms or integration strategies. Nor is any attempt made to select between competing models of magnetic, olfactory, sun-related or visual navigation. These exclusions do not constitute a deficiency, but a deliberate restriction arising from the formulation of Research Question 2 and the chosen experimental reduction of the configuration design.

The reach of the results is confined to the experimental framework described in §5.5. The manipulations concern controlled variation in the availability of distinct cues under specific field conditions. Generalisation to other geographical regions, extreme climatic conditions or natural migratory contexts falls outside the scope of this chapter. In particular, the conceptual limit case of complete sensory reduction discussed in Chapter 1 is not realised empirically here.

The functional contribution of this chapter is therefore epistemically constraining. It establishes the extent to which assumptions concerning necessity, dominance and compensation are descriptively supported or qualified within the limits of the experiment conducted. Where reduction of individual cues does not abruptly disorganise the return pattern but produces proportional shifts, homing behaviour remains robust within these limits of variation without any single cue having to be regarded as strictly constitutive. At the same time, the findings show the extent to which performance changes when multiple information sources are reduced simultaneously.

This definition of scope provides the necessary point of departure for the continuation of the empirical research. Whereas this chapter addresses variation of individual navigational cues, Chapter 6 shifts the focus towards a broader problematisation of homing behaviour in which the central concern is not any single cue, but the stability of return patterns under more complex and ecologically plausible variation. The analysis thereby moves from testing assumptions concerning individual information sources in Research Question 2 to answering Research Question 3.

Chapter 6 – Answering Research Question 3: Sustained Performance under Combined Variation

6.0 Introduction: Theoretical Elaboration and Positioning

In Chapter 1, the phrase ‘pigeons in the Arctic night’ was introduced as a constructed limit case: a hypothetical condition in which familiar navigational information sources are simultaneously and substantially reduced. The phrase had no empirical status there, but served as an analytical device for revealing the scope of explanatory models. Chapter 5 subsequently examined how homing behaviour changes when individual navigational cues are varied systematically. Within the limits of variation employed, no individual cue proved strictly constitutive of goal-directed return behaviour.

The shift in this chapter therefore concerns not the contribution of individual information sources once again, but the question of how the homing system as a whole functions when multiple information sources are restricted simultaneously. Research Question 2 concerned cue-specific sensitivity; Research Question 3 concerns changes in performance under cumulative uncertainty. The object of assessment thereby shifts from element-level analysis to system behaviour under system pressure.

The literature on pigeon navigation has traditionally focused strongly on individual information sources: magnetic information (Wiltschko & Wiltschko), olfactory information (Papi; Wallraff), sun-related information (Kramer) and visually guided routes (Biro; Guilford). These research programmes have demonstrated convincingly that manipulation of specific cues can produce measurable effects on departure orientation and return. Less systematic attention has been devoted, however, to how these information sources function jointly when several are restricted simultaneously. Redundancy is often assumed, but is rarely evaluated under controlled cumulative reduction.

Within the broader perceptual literature, multisensory integration has been described as a process in which information sources are combined according to their relative reliability (Ernst & Bülthoff, 2004). This principle of cue weighting implies that the contribution of individual signals changes dynamically according to their contextual quality. Neuroscientific research on the integration of visual and vestibular information confirms that weights are adjusted adaptively when signal reliability changes (Angelaki, Gu, & DeAngelis, 2009; Fetsch et al., 2012). Applied to homing behaviour, this suggests that disruption of one cue need not result in performance loss, but may instead produce a redistribution of informational value among the sources that remain available.

The transfer of such integration models to large-scale navigation is not self-evident, however. Navigation does not depend solely on the simultaneous integration of signals, but also involves spatial representation, experience and environmental structure (Jacobs & Schenk, 2003; Cheng & Spetch, 2011). The question is therefore not merely whether cue weights change, but whether cumulative reduction within realistic limits of variation produces proportional or non-linear changes in performance.

The literature on robustness in biological systems provides an additional framework. Robustness refers to the capacity of systems to remain functionally stable under disturbance, although this capacity is not unlimited (Kitano, 2004). Complex systems may respond proportionately within certain margins, but in some cases undergo abrupt shifts when critical thresholds are exceeded (Scheffer et al., 2001). Applied to homing behaviour, this raises the question whether cumulative reduction of navigational cues produces gradual changes in performance or a threshold-like loss of goal-directed behaviour.

The experiment in this chapter operationalises this problem. Rather than isolating individual cues, multiple cue dimensions are varied simultaneously according to a predefined configuration structure. The aim is not to identify an underlying mechanism, but to establish empirically whether homing performance continues to change gradually under combined variation or displays a limiting condition. Where changes in performance remain proportional, this supports a descriptive account of robustness. Where a disproportionate decline becomes apparent, by contrast, a system boundary becomes empirically identifiable.

The metaphor of the Arctic night functions here exclusively as a theoretical reference point. The experiment does not seek to realise this extreme condition, but investigates how far cumulative reduction can be increased within ethically proportionate limits without loss of functional coherence. Research Question 3 is thereby positioned as a systematic test of robustness under cumulative uncertainty, substantively distinct from but logically building on the element-level analysis conducted in Chapter 5.

6.1 Central Assumptions

The shift from variation of individual cues to cumulative system pressure requires the assumptions addressed in Research Question 3 to be reformulated. These assumptions no longer concern the necessity of individual information sources, but the form of behavioural change when the reliability of multiple sources is reduced simultaneously.

A first assumption, implicit in parts of the navigation literature, is that homing behaviour depends on the redundant integration of multiple information sources. According to this view, the system can absorb performance loss because alternative cues assume functional contributions when a dominant source becomes temporarily unreliable. This reasoning is consistent with broader models of multisensory integration in which the relative reliability of signals is weighted dynamically through cue weighting. In such models, disruption of one source primarily produces a redistribution of contributions rather than behavioural collapse.

A second, more stringent assumption concerns the existence of system boundaries. Even where integration is dynamic and context-dependent, cumulative reduction of information may be assumed to reach a point at which goal-directed behaviour declines disproportionately. From this perspective, robustness is not an unlimited property, but condition-dependent stability within specific limits of variation.

A third possible position rejects both strong redundancy and sharply defined collapse points, and assumes that changes in performance under cumulative uncertainty remain proportional and gradual. In that case, no clear limiting condition can be identified within the experimental range; behavioural variation remains distributed along a continuum.

The experiment in this chapter was not designed to confirm any one of these assumptions as an explanatory model. It was designed to determine which of these descriptive hypotheses prove necessary to characterise adequately the observed patterns under combined variation. The experiment thereby tests explicitly whether the widely used concept of 'robustness' is descriptively justified in the context of homing behaviour, or merely constitutes an interpretative shorthand for partial findings from studies involving manipulation of individual cues.

6.2 Conceptual Operationalisation of Combined Variation

Chapter 5 examined what happens when individual navigational cues are reduced. In each condition, one cue was manipulated. The question there was whether a specific information source is necessary for goal-directed homing behaviour. In this chapter, the cues under investigation do not change; what changes is the number of cues reduced simultaneously. Combined variation means that several information sources are restricted at the same time within a single flight. The number of simultaneously reduced cues is increased systematically. First one cue is restricted, as described in the previous chapter, then two, and subsequently three. This creates an ascending sequence of information restriction.

This ordering makes it possible to examine how homing behaviour changes as the overall information environment becomes less stable. The question is no longer whether a specific cue is necessary, but how behaviour develops when several sources become less reliable simultaneously. The most extreme conceivable situation, in which none of the identified cues is available, is not implemented as an experimental condition. It serves solely as a hypothetical boundary marking the point that information restriction cannot be increased indefinitely. The experiment remains limited to configurations that are practicable and proportionate.

This operationalisation places the relationship between the degree of information restriction and behavioural change at the centre of the analysis. Whether performance changes gradually or displays a distinct transition is an empirical question addressed in the following sections.

6.3 Assumption Structure and Design

The design in this chapter is derived directly from the assumption structure formulated in Chapter 3. It was established there that explanatory models of homing behaviour often implicitly assume the necessity, dominance and compensation of individual navigational cues. Chapter 5 examined the extent to which such assumptions remain tenable under separate variation of information sources. This chapter examines how these assumptions relate to the cumulative reduction of multiple cues.

The design consists of a series of predetermined conditions in which several navigational cues are reduced simultaneously. The conditions were selected so that the number of cues manipulated at the same time increases systematically. This increase constitutes the experimental variable: not the nature of the cue, but the number of information sources reduced simultaneously. The design retains the within-subject structure used in Chapter 5. The same individuals undergo all conditions according to a predetermined randomisation schedule. This prevents differences in baseline performance between individuals from distorting comparisons between conditions.

The decision to restrict the number of conditions to a reduced set is methodologically motivated. Not all theoretically possible combinations of cue reduction are implemented. Only those configurations necessary to establish whether cumulative reduction leads to proportional performance change or to a disproportionate decline in return are included. This confines the experiment to epistemically relevant variation and avoids unnecessary burden on the animals.

The design makes it possible to distinguish empirically between three descriptive positions identified in Chapter 3. First, it can be established whether homing behaviour remains stable when several cues are reduced simultaneously, which would be compatible with strong compensation assumptions. Second, it can be examined whether performance loss increases proportionally as more cues are reduced. Third, it can be assessed whether a distinct boundary becomes visible within the range investigated, at which homing patterns change abruptly.

The experiment is therefore not aimed at identifying one decisive mechanism, but at determining the form of behavioural change under increasing information restriction. This form — proportional or disproportionate — constitutes the central object of assessment for Research Question 3.

6.4 Implementation Protocol

This chapter examines only configurations in which two or three navigational cues are manipulated simultaneously. The control condition and the four individual cue manipulations were implemented in Chapter 5 and are not repeated here. Condition codes C5–C9 continue numerically from C0–C4 but belong to a separate experiment.

The same thirty adult homing pigeons that participated in the Chapter 5 experiment take part in this experiment. The independent biological unit of analysis therefore remains the individual pigeon, and the population size is N = 30. Each pigeon undergoes each of the five combined configurations once. Thirty test flights are consequently available per configuration, producing a complete dataset of 150 test flights. Four configurations contain two simultaneous cue manipulations and are designated reduction level D2. One configuration contains three simultaneous manipulations and is designated reduction level D3.

Condition code	Magnetic	Olfactory	Sun	Visual	Level
C5	0	0	1	1	D2
C6	0	1	0	1	D2
C7	1	0	0	1	D2
C8	1	1	0	0	D2
C9	0	0	0	1	D3

Table 6.4a. Configuration structure under combined cue manipulation

A value of 1 denotes availability without experimental manipulation; a value of 0 denotes application of the manipulation described in §5.4. The coding does not mean that a sensory information source is biologically entirely present or absent. The four D2 configurations do not provide full factorial coverage of all six possible two-cue combinations. Results at D2 level therefore relate exclusively to the four configurations implemented and must not automatically be generalised to every possible two-cue manipulation.

Implementation follows the same within-subject principle as in Chapter 5. Each pigeon flies once under each configuration and once from each release distance; no pigeon flies twice under the same configuration or twice from the same release site. The five release distances are 86, 88, 90, 92 and 94 kilometres. Each combination of condition and distance occurs six times, resulting in a mean release distance of exactly 90 kilometres in every condition. Configuration, distance and order of implementation are counterbalanced. At least eleven days separate two test flights by the same pigeon.

The individual manipulations are technically implemented as described in §5.4. The only difference from Chapter 5 is the simultaneous application of two or three manipulations within the same test flight:

Pigeons	Flight 1	Flight 2	Flight 3	Flight 4	Flight 5
D1–D6	C5	C7	C9	C6	C8
D7–D12	C6	C8	C5	C7	C9
D13–D18	C7	C9	C6	C8	C5
D19–D24	C8	C5	C7	C9	C6

Pigeons	Flight 1	Flight 2	Flight 3	Flight 4	Flight 5
D25–D30	C9	C6	C8	C5	C7

Table 6.4b. Counterbalancing of the condition sequence in Chapter 6

Under this arrangement, C9, the three-cue reduction, is not systematically implemented after the D2 configurations. Like every other configuration, C9 occurs six times in each sequence position. Any difference between D2 and D3 therefore cannot readily be attributed to fatigue, experience or the point at which the test flight occurred within the experimental sequence.

The observation period is again 240 minutes. A return value of 0 indicates only that no arrival was registered within this time window. It does not necessarily mean that the pigeon ultimately failed to return to the home loft. GPS trajectories remain separately available for calculating initial orientation deviation and route index.

6.5 Assessment Protocol and Data Processing

The same four performance indicators as in Chapter 5 are used: 1) return within 240 minutes; 2) homing time; 3) initial orientation deviation and 4) route index. The operational definitions set out in §5.5.3 remain unchanged. Homing time is calculated only for test flights in which an arrival was registered within the observation window. A non-timely return is not assigned a fictitious homing time of 240 minutes. Return percentage and homing time must therefore always be assessed jointly.

The analysis is first conducted by configuration. Conditions C5–C9 each contain thirty test flights by thirty different pigeons. This allows differences between the four D2 configurations to remain visible and prevents D2 from being treated incorrectly as a completely homogeneous condition.

The configurations are then grouped by reduction level. Level D2 comprises conditions C5–C8 and therefore 120 test flights; Level D3 comprises C9 and therefore 30 test flights. The number of test flights is not equivalent to the number of independent biological units of analysis. Although D2 contains 120 homing episodes, these originate from the same thirty pigeons. The biological sample therefore remains N = 30 at D2 level.

For the comparison of C0, D2 and D3, one value per level is calculated for each pigeon. For C0 and D3, this is the individual test flight completed by the animal concerned. For D2, the mean across the four D2 configurations is calculated for each pigeon. The comparison between the three levels is therefore based on the same thirty animals. Because every pigeon completes the same number of D2 test flights, the rounded group means correspond to the means calculated across all 120 D2 episodes.

Performance decline relative to C0 is present when one or more of the following directional changes occur: a lower return percentage; a longer homing time; a lower route index; a greater initial orientation deviation. A cumulative pattern is present when D2 performs less favourably on average than C0 and D3 performs less favourably on average than D2. Such an ordering does not demonstrate that the number of manipulated cues alone caused the difference. Differences between the specific cue configurations remain relevant.

The assessment remains descriptive. A gradual shift is distinguished from an abrupt discontinuity, but no direct claims about internal compensation, cue weighting or other navigational mechanisms are derived from the results.

6.6 Results

The dataset comprises 150 test flights by thirty pigeons. Each pigeon underwent four D2 configurations and one D3 configuration. D2 therefore comprises 120 test flights and D3 30 test flights. The complete data are presented in Appendix B.

6.6.1 Raw Data per Homing Episode

Each row in Appendix B corresponds to one individual test flight. The extract below presents the five combined configurations completed by D1. The differences in release distance within this individual example form part of the counterbalanced design; at population level, every configuration has the same distance distribution.

Episode	Pigeon	Condition	Level	Distance (km)	M	O	S	V	Return	Time (min)	Deviation (°)	Route index
E151	D1	C5	D2	86	0	0	1	1	1	81.22	33.30	0.705
E181	D1	C6	D2	88	0	1	0	1	1	79.34	28.08	0.742
E211	D1	C7	D2	90	1	0	0	1	1	87.90	40.03	0.676
E241	D1	C8	D2	92	1	1	0	0	1	88.43	32.32	0.695
E271	D1	C9	D3	94	0	0	0	1	1	102.20	47.38	0.616

Table 6.6.1 raw data homing episodes (extract)

6.6.2 Aggregated Performance by Configuration

For each configuration, the return percentage, mean homing time, standard deviation, mean route index and mean initial orientation deviation were calculated. Homing time relates only to timely homing episodes. The remaining trajectory measures are based on the available GPS recordings.

Condition	Level	N	Return (%)	Mean time (min)	Time SD	Mean route index	Mean deviation
C5	D2	30	90.0	87.9	3.9	0.690	34.6°
C6	D2	30	96.7	82.6	3.4	0.737	28.1°
C7	D2	30	90.0	92.1	4.2	0.655	41.8°
C8	D2	30	93.3	88.8	2.9	0.682	35.3°
C9	D3	30	86.7	100.9	3.7	0.597	51.6°

Table 6.6.2 Aggregated performance indicators by configuration

There is clear variation between configurations within D2. C6 approaches the performance level of the individual manipulations examined in Chapter 5, whereas C7 has the longest mean homing time, the lowest route index and the greatest initial deviation within D2. The number of simultaneous manipulations is therefore not the only relevant ordering variable; the composition of the configuration is also associated with performance. C9 performs less favourably than the mean of the four D2 configurations on all four indicators. At the level of central values, this produces a cumulative ordering without eliminating the heterogeneity within D2.

6.6.3 Comparison with the Control Condition

For the assessment of cumulative performance decline, C0 from Chapter 5 is used as the reference condition. The same thirty pigeons provide the observations for C0, D2 and D3.

Level	N	Flights	Return (%)	Mean time (min)	Time SD	Mean route index	Mean deviation
C0	30	30	100.0	70.9	3.2	0.866	11.3°
D2	30	120	92.5	87.8	5.0	0.691	35.0°
D3	30	30	86.7	100.9	3.7	0.597	51.6°

Table 6.6.3. Performance indicators for C0, D2 and D3

All indicators show the same direction: C0 performs more favourably than D2, and D2 performs more favourably than D3. The decline concerns not only return and homing time. As reduction increases, routes become less direct on average and initial course deviation increases.

6.6.4 Differences and Dispersion

The differences relative to the control condition (C0) are as follows:

Comparison	Δ return	Δ time	Δ route index	Δ initial deviation
D2 relative to C0	−7.5 percentage points	+16.9 min	−0.175	+23.6°
D3 relative to C0	−13.3 percentage points	+29.9 min	−0.269	+40.2°
D3 relative to D2	−5.8 percentage points	+13.1 min	−0.094	+16.6°

Table 6.6.4. Differences between reduction levels

The performance shift increases further under D3, but dispersion does not increase correspondingly for every indicator. The standard deviation of homing time is 5.0 minutes under D2 and 3.7 minutes under D3. A general claim that D3 produces greater variability is therefore not justified.

The ranges overlap partially: homing time, D2 77.4–100.6 minutes and D3 92.1–106.5 minutes; route index, D2 0.56–0.75 and D3 0.50–0.63; initial deviation, D2 22.3–60.8° and D3 44.0–71.8°. This overlap indicates a gradual shift in the distributions rather than complete separation between D2 and D3. At the same time, the central values for D3 consistently fall on the less favourable side of D2.

6.6.5 Logical Link to Research Question 3

Research Question 3 concerns the form of performance change when multiple navigational cues are manipulated simultaneously. Relative to C0, D2 is associated with a lower return percentage, a longer homing time, less direct routes and greater initial course deviation. Under D3, all four indicators shift further in the same direction.

Within the range investigated, cumulative performance degradation is therefore present. This degradation does not, however, have an all-or-none character. Under D3, 86.7% of the pigeons return within the observation window, and recognisably goal-directed route patterns remain present. No collective disorganisation or abrupt loss of performance is observed.

At the same time, the differences between configurations within D2 constrain a purely numerical interpretation. Performance is associated not only with the number of manipulated cues, but also with their specific combination. The results therefore support a description in which homing behaviour becomes gradually less efficient under cumulative information restriction, without an empirical breakpoint occurring within the configurations implemented.

This behavioural ordering does not reveal which information sources are internally reweighted or which compensatory mechanism is active. The results constrain explanatory assumptions but do not identify an underlying navigational mechanism.

6.7 Scope and Link to Chapter 7

The sole purpose of this chapter has been to describe pigeon homing behaviour under cumulative reduction of multiple navigational cues. Unlike Chapter 5, which focused on individual information sources, the present chapter concerned the form of performance change when multiple cues were reduced simultaneously. The data organised in §6.6 permit assessment of whether behavioural change proceeds proportionately or displays a clear discontinuity within the range investigated.

The results leave open which internal processes or integration strategies underlie the observed patterns. No claims are made concerning the dynamic redistribution of informational values, internal representations or decision-making mechanisms. Nor is any attempt made to select between alternative explanatory models of navigation. This restriction follows from the formulation of Research Question 3 and the experimental design employed.

The reach of the findings is confined to the configurations of two-cue and three-cue reduction described in §6.4. The extreme limit case involving complete reduction of all identified cues is not realised empirically and falls outside the scope of this chapter. No generalisations are made to other distances, geographical conditions or natural migratory contexts.

The functional contribution of this chapter is therefore constraining in nature. It establishes whether, and to what extent, homing behaviour under cumulative information restriction remains within proportional limits of variation or shows indications of a boundary within the range investigated. This finding provides the necessary point of departure for Chapter 7, in which the patterns identified here are considered in relation to competing explanatory models and the broader problem of explanatory pluralism.

Chapter 7 – Answering Research Question 4: Minimal Explanatory Assumptions

7.0 Introduction: Positioning Research Question 4

Research Question 4 — 'Which assumptions about internal processing prove necessary to understand the observed performance, and which assumptions can be relinquished without losing explanatory coherence?' — differs in nature from the preceding research questions. Whereas Chapters 4 to 6 focused on behavioural outcomes under controlled variation, Research Question 4 concerns an analytical assessment of explanatory models in the light of the results already obtained. No additional data are collected and no new experimental condition is introduced.

The empirical chapters, Chapters 4 to 6, examined the extent to which assumptions concerning necessity, dominance and hierarchical ordering were descriptively required to characterise the observed behavioural variation. This made clear that sustained performance under variation does not automatically compel strong assumptions concerning exclusive mechanisms.

This chapter systematically relates the findings from Research Questions 1 to 3 to the status of these assumptions. The aim is not to identify a single decisive model, but to establish the extent to which assumptions prove necessary, unnecessary or indeterminate within the range investigated.

7.1 Empirical Findings from Research Questions 1–3

The empirical studies presented in Chapters 4 to 6 reveal a consistent pattern. For Research Question 1, classification performance changed proportionately under systematic variation of stimulus features, without abrupt collapse within the range investigated. Both exemplar-specific and non-exemplar-specific descriptions remained empirically compatible with the observed data.

For Research Question 2, reduction or manipulation of individual navigational cues produced measurable shifts in return rate and return time, but did not result in systematic loss of goal-directed return behaviour within the range investigated.

For Research Question 3, cumulative reduction produced further changes in performance without revealing a clear limiting condition in which goal-directed behaviour disappeared abruptly.

Taken together, these findings indicate a pattern in which behavioural change remains proportional under variation and displays no clear discontinuity within the configurations employed.

7.2 Pressure on Assumptions of Necessity and Dominance

Chapter 3 identified explanatory models in which assumptions concerning necessity, dominance and the hierarchical ordering of information sources play a central role. These assumptions imply that sufficient reduction of relevant information should produce a qualitative shift in behaviour, or that disruption of a dominant cue should lead to systematic and non-gradual performance loss.

The empirical patterns from Research Questions 1 to 3 place these assumptions under pressure. In none of the domains investigated was an abrupt transition identified within the range employed at which behaviour became structurally disorganised. Behavioural change remained proportional to the degree of manipulation under variation of stimulus features and under reduction of individual or multiple navigational cues.

This pattern reduces the descriptive necessity of strong assumptions concerning exclusive necessity. Where goal-directed behaviour continues despite reduction of an individual information source, necessity in the strict sense cannot simply be maintained. Nor does a stable hierarchical dominance of one cue become unambiguously apparent within the range investigated.

This does not, however, entail the elimination of the explanatory models concerned. The empirical findings do not exclude the existence of dominant or necessary mechanisms; they merely constrain the extent to which such assumptions are descriptively indispensable for characterising the observed behaviour. Models in which multiple information sources contribute simultaneously remain empirically compatible within these limits.

The tension identified here therefore concerns not the possibility of particular mechanisms, but the extent to which strong assumptions concerning necessity and dominance are compelled by the available behavioural data.

7.3 Systematic Ordering of Assumption Structures

The preceding sections examined, for each research question, which assumptions were placed under empirical pressure. To structure the answer to Research Question 4, these findings are ordered explicitly below. The concern is not the confirmation or refutation of explanatory models as a whole, but the status of individual assumptions within the experimental framework employed.

'Necessary' refers here to an assumption whose removal results in loss of the descriptive coherence of the observed behaviour. 'Unnecessary' refers to an assumption that can be relinquished without rendering sustained performance inexplicable. 'Indeterminate' refers to an assumption whose status could not be established unambiguously within the chosen design.

Domain	Assumption investigated	Empirical status within this design	Explanation
Classification (RQ1)	Performance requires storage of individual stimulus presentations	Unnecessary	Sustained performance occurred under variation in which stimulus identity was altered
Classification (RQ1)	Performance requires a summary prototype	Indeterminate	The data are compatible with both exemplar-based and prototype-based descriptions

Domain	Assumption investigated	Empirical status within this design	Explanation
Homing (RQ2)	A specific cue is strictly necessary	Unnecessary	Reduction of individual cues did not result in performance collapse
Homing (RQ2)	Disruption of a dominant cue produces proportional performance loss	Partially tenable	Gradual shifts were observed, but exclusive dominance could not be demonstrated
Homing (RQ3)	Cumulative reduction produces threshold-like behaviour or collapse	Not demonstrated within the limits of variation	Changes in performance remained proportional
Homing (RQ3)	System behaviour depends on redundant integration	Compatible, but not exclusive	Alternative descriptions could not be eliminated

Table 7.3. Status of the Assumptions Investigated within the Experimental Framework

This ordering shows that the empirical studies in this dissertation did not eliminate explanatory pluralism, but differentiated the status of the assumptions involved. Some assumptions proved unnecessary within the design employed; others remained compatible with the data without being confirmed exclusively.

The answer to Research Question 4 therefore does not consist of selecting a single explanatory model, but of making explicit the assumption structure constrained by the empirical material.

7.4 Explanatory Pluralism within the Investigated Range (Condensed)

The ordering presented in Table 7.3 shows that, within the experimental framework employed, multiple explanatory frameworks remain descriptively compatible with the same behavioural data. In none of the domains investigated was a behavioural discontinuity identified that empirically compelled the exclusive selection of a single explanatory structure.

This finding is strictly confined to the range investigated. No claims are made concerning possible limiting conditions outside the variation employed or the extent to which alternative experimental configurations might permit further differentiation. The pluralism established here concerns exclusively the relationship between the dimensions of variation applied and the observable behavioural outcomes.

7.5 Methodological Implications for Assessability

Where multiple explanatory models remain descriptively adequate within the same experimental range, the assessment question shifts from comparing performance outcomes to making assumption structures explicit. The empirical chapters have shown that variation of stimulus features and navigational cues does not compel the unambiguous elimination of explanatory approaches.

Assessability thereby acquires a procedural dimension: the central criterion is not the degree of sustained performance as such, but the extent to which assumptions are explicit, distinguishable and empirically addressable. Research Question 4 therefore concerns not the selection of a best-performing model, but the systematic ordering of the status of assumptions within the range investigated.

7.6 Scope and Link to Chapter 8

This chapter has introduced no new empirical data and has selected no explanatory model. The analysis was confined to making explicit which assumptions prove necessary, unnecessary or indeterminate within the range investigated. The reach of these findings is limited to the experimental framework of Chapters 4 to 6. No claims are made concerning possible limiting conditions outside this range or other behavioural domains or species.

On the basis of this ordering, Chapter 8 formulates the explicit answer to Research Question 4.

Chapter 8 – Conclusion, Discussion and Further Research

8.1 Answers to the Research Questions and Synthesis

This section first answers the individual research questions on the basis of the findings reported in Chapters 4 to 7. Following a synthesis of these findings, the central research question is then answered.

8.1.1 Research Question 1 – Pattern Recognition and Classification

The findings concerning classification behaviour show that homing pigeons continue to display stable response frequencies under controlled variation of stimulus exemplars within predefined task formats. The introduction of novel, non-identical exemplars produces measurable but limited shifts in response distributions, without causing classification behaviour to disintegrate. Sustained performance therefore does not depend on the exact repetition of previously presented stimuli.

At the same time, the empirical material does not compel the assumption of abstract, linguistic or semantically interpreted representations. The data show that strictly exemplar-specific binding is insufficient to describe the behaviour fully, but do not resolve the underdetermination between exemplar-based and more global descriptive frameworks.

Research Question 1 can therefore be answered affirmatively, but with qualifications: classification behaviour remains stable under variation, without this stability reducing to one necessary explanatory framework.

8.1.2 Research Question 2 – Decision-Making under Variation of Individual Navigational Cues

The field studies involving variation in individual navigational information sources show that homing performance shifts gradually when specific information sources are restricted or modified. Return percentages and mean homing times change systematically, but remain within a range in which goal-directed behaviour is preserved. None of the individually examined cues proves strictly necessary for the occurrence of homing behaviour within the range investigated. Several conditions display a consistent and proportional performance shift.

Initial orientation deviation shows a strong positive association with homing time. After adjustment for mean differences between conditions, a smaller but still statistically significant positive association remains. Controlling for release distance likewise does not alter the direction of this relationship.

Research Question 2 can therefore be answered in terms of gradual sensitivity: decision-making under variation in individual navigational information sources remains functionally reliable, while the exclusive necessity of any single cue is not empirically compelled.

8.1.3 Research Question 3 – Sustained Performance under Combined Variation

Under combined manipulation, a cumulative performance shift is observed. The return percentage declines, mean homing time increases, routes become less direct, and mean initial orientation deviation increases. Under D3, however, 86.7% of the pigeons still return within the observation window. No all-or-none transition therefore occurs within the configurations investigated.

Cumulative pressure thus leads to performance degradation, but not to complete collapse. Even under increased system pressure, homing behaviour remains recognisable as a goal-directed pattern. Explanatory pluralism is not confined to isolated variations, as examined in Chapter 5, but persists under the combined burden examined in Chapter 6.

Research Question 3 is therefore answered in terms of robust but bounded degradation: multiple assumption structures remain empirically compatible, even when several hypothesised mechanisms are placed under pressure simultaneously.

8.1.4 Research Question 4 – Assessability of Explanatory Models

On the basis of the empirical findings from Research Questions 1 to 3, it can be established that explanatory models remain difficult to eliminate in relation to one another as long as they remain compatible with the sustained performance observed within the investigated domain of variation.

Making assumptions explicit reveals which elements prove unnecessary, but does not reduce the field to one dominant model. Within the experimental range employed, explanatory pluralism in this domain is not merely a temporary consequence of limited data, but a structural feature of the relationship between behavioural stability and explanatory structure as investigated here (cf. Mitchell, 2002).

8.1.5 Synthesis – Answer to the Central Research Question

The central research question was: ‘To what extent can homing pigeons make consistent and reliable behavioural decisions under structural uncertainty, without explicit semantic understanding or transparent internal representations?’

The findings show that homing pigeons continue to display robust performance under variation of individual navigational cues, as examined in Chapter 5, and under cumulative variation, as examined in Chapter 6. None of the assumptions investigated concerning internal representations proves strictly necessary on the basis of the empirical evidence.

Reliable behavioural outcomes therefore appear possible without complete explanatory transparency being empirically attainable. The most robust result of this research is not the confirmation of a single explanatory model, but the persistence of performance under explanatory pluralism within the range investigated. In this domain, sustained performance does not coincide with explanatory reduction.

8.2 Discussion

8.2.1 Underdetermination as an Empirical Outcome: Trivial or Delimited?

An obvious criticism is that the underdetermination identified here is hardly surprising. Biological systems are redundant, adaptive and multicausal. From the perspective of complexity and systems theory, explanatory pluralism may therefore be expected. This line of reasoning, however, operates at an abstract level. The fact that systems may be multicausal does not imply that explanatory reduction is impossible within a specific empirical domain.

It was not known in advance to what extent redundancy would provide functional compensation, whether cumulative disruption would produce abrupt collapse, or whether one information source would nevertheless prove dominant under combined pressure. The contribution of this research therefore lies not in confirming complexity as such, but in empirically delimiting its effects: within the parameter range investigated, systematic variation does not eliminate explanatory pluralism. Underdetermination is thus not a tautological inference from system complexity, but an empirically situated outcome.

8.2.2 Internal Validity: Where Does the Design Come under Strain?

The research design was assumption-driven and was not constructed as a competitive model-selection experiment. This choice made it possible to test assumptions proportionately without destabilising the behavioural system. At the same time, this approach introduces a tension. Gradual variation can reveal pluralism, but may also stabilise it. Extreme parameter values were not investigated; a possible threshold or collapse outside the range examined therefore cannot be excluded. The conclusion of 'no elimination' applies explicitly within the variation domain employed.

A second issue concerns the operationalisation of 'performance'. In this study, performance was defined behaviourally in terms of return percentage, orientation deviation, homing time, route index and response frequency. These measures are reproducible, but reduce the phenomenon to quantifiable outcomes. More fine-grained trajectory data or physiological measurements might have produced stronger model differentiation. The observed underdetermination therefore applies at the level of this behavioural construct. Internal validity is consequently strong within the chosen design, but its scope is partly determined by the choices made in the interests of proportionality.

8.2.3 Reliability: Stability versus Homogeneity

Reliability was understood in this study as pattern stability rather than homogeneity. The within-subject design shows that individual pigeons respond differently to changes in cue configuration. Because each pigeon undergoes each condition only once, the stability of individual behavioural profiles within the same condition cannot be established. The design does, however, partially control for interindividual differences in baseline performance because the same animals are examined under all conditions.

This heterogeneity increases ecological plausibility, but complicates interpretation. Pluralism may partly result from population-level differences in strategy configuration. Although the repeated-measures design addresses interindividual differences, individual-level analysis might still reveal sharper model differentiation. In addition, repeated exposure to variation may have initiated subtle reweighting of information sources. The observed stability may therefore partly depend on adaptive reconfiguration of information sources during the experiment. This strengthens the interpretation of flexibility, but makes it more difficult to distinguish between structural and dynamic pluralism.

8.2.4 Interpretative Pressure Points

The central claim — the persistence of explanatory pluralism despite systematic variation — rests on three explicit assumptions. First, the selected behavioural measures are assumed to be adequate for recording relevant sustained performance. Where more fine-grained data would produce stronger differentiation between models, pluralism may partly be a function of measurement resolution.

Second, the representativeness of the variation configurations is decisive. The absence of collapse under combined variation is interpreted as robustness within ecologically plausible limits. This does not imply that explanatory reduction beyond those limits is impossible in principle.

Third, the research programme was directed towards testing whether reduction was empirically compelled, rather than towards competitive model elimination. The data show that reduction is not compelled within this framework; they do not demonstrate that reduction is impossible under every conceivable condition.

8.2.5 Synthesis of the Discussion

Taken together, the findings support a proportionate conclusion. The research demonstrates robustly sustained performance and persistent explanatory pluralism within the investigated ranges of variation. Assumptions are constrained, but not eliminated. Extreme parameter values were not investigated, measurement resolution remained behavioural, population heterogeneity may reinforce pluralism, and reduction outside the investigated range remains theoretically conceivable.

These limitations do not undermine the central conclusion, but situate it. The outcome is not a general claim about biological complexity, but an empirically delimited finding: within this design, under these configurations and at this behavioural level, sustained performance persists without explanatory reduction.

8.3 Recommendations for Further Research

The findings of this dissertation have not eliminated explanatory pluralism, but have constrained it within a specific range of variation and level of measurement. The limitations discussed in §8.2 — the range of variation, behavioural resolution and population structure — therefore serve not only to qualify the findings, but also to direct further research.

A first line of inquiry concerns the systematic exploration of parameter boundaries. The present design employed gradual and proportionate variation. Possible critical transition points were therefore not reached. Future research could examine explicitly whether parameter values exist at which pluralism gives way to sharper differentiation between models, or whether robustness persists under greater system pressure.

A second line concerns refinement of the level of measurement. Performance was operationalised here in behavioural and relatively global terms. More fine-grained trajectory analysis or real-time modelling of course corrections could establish whether subtle differences between assumption structures become visible at a higher level of resolution — or whether multiple descriptions remain compatible even at that level.

A third line concerns analysis at the individual level. Where individual animals consistently employ different strategy configurations, pluralism may partly constitute a population-level effect. Where multiple descriptions remain tenable even at the individual level, this would indicate more deeply rooted systemic underdetermination.

Research at other levels of description — physiological, neural or computational — could additionally establish whether explanatory reduction becomes more apparent below the behavioural level. Finally, a comparative approach could determine whether the pattern identified here is domain-specific or occurs more broadly in complex adaptive systems. Further research should therefore focus not primarily on identifying a single dominant model, but on determining the conditions under which reduction becomes empirically compelling — or fails to do so.

8.4 Concluding Reflections

This research has produced neither an all-encompassing explanatory model nor a reduction of the existing explanatory frameworks. It has, however, shown the conditions under which robust behaviour can persist without a proportionate increase in explanatory transparency.

Within the domain investigated, stability and underdetermination prove to be simultaneous characteristics of the same system. This finding remains empirically confined to the variation configurations employed and the behavioural level selected.

The broader implication concerns the relationship between functioning and understanding: reliable performance does not necessarily imply explanatory reduction. The epilogue develops this tension further, shifting the focus from the specific behavioural domain to more general characteristics of systems in which performance is compelling while explanation remains constrained.

Epilogue – On Performance, Explanation and System Architecture

I. 'Epistemological Generalisation'?

At first sight, this dissertation has confined itself to a behavioural-biological domain: classification and navigation in homing pigeons under controlled variation. Its central result was formulated soberly. Performance proved robustly sustained, while explanatory reduction failed to occur. Under systematic pressure, assumptions were constrained but not eliminated. Pluralism persisted.

What may initially be read as a domain-specific finding invites broader reflection on closer examination. The combination of three characteristics — redundant integration of multiple information sources, adaptive reweighting under variation and stable behavioural outcomes — appears to identify a type of system in which performance and explanatory transparency do not necessarily coincide. In such systems, behaviour is reliable and reproducible, while the internal organisation remains only partially reducible to a single explanatory framework. This is not a deficiency of research, but an indication that the relationship between functioning and understanding is less linear than is often assumed. Reduction is not excluded in principle, but in practice proves constrained by the way in which the system is organised.

The homing pigeon therefore functions in this dissertation less as an object of wonder than as a concrete example of an architecture in which multiple information channels can compensate for one another and in which adaptivity arises through exposure to variation. Performance is not sustained by a single dominant axis, but by interaction among heterogeneous contributions. It is precisely this heterogeneity that makes the system robust — and simultaneously resistant to simple explanatory reduction.

This tension is not confined to biological systems. Systems also exist outside the organic domain whose performance is compelling while their internal dynamics remain only partially transparent. In particular, systems that learn through large-scale exposure to variation and base their functioning on the statistical reweighting of heterogeneous input sources display a comparable structure: they produce stable outcomes without any single explanatory model being wholly adequate to describe their behaviour.

The parallel does not imply identity. Biological and artificial systems differ in material constitution, evolutionary history and implementation. They nevertheless share an architectural characteristic: robust performance can arise from redundancy, large-scale exposure and adaptive integration without complete internal explainability being a precondition for functioning.

This raises a broader epistemological question. Where system types exist in which sustained performance is structurally associated with explanatory pluralism, underdetermination cannot be understood solely as a temporary lack of knowledge. In some cases, it may be an emergent property of the architecture itself. The question then shifts from 'Which model is correct?' to 'Under which conditions can reduction realistically be expected?'

For the design of future systems — whether biologically inspired or artificial — this implies that robustness and explainability do not necessarily develop in parallel. Systems optimised for adaptivity under variation may prove resistant to explanation precisely because they lack a hierarchically unitary structure. This is not a normative claim about desirability, but an analytical observation concerning the relationship between architecture and knowability.

The empirical study of homing-pigeon behaviour has made this tension visible within a concrete natural-scientific framework. It does not claim to provide a general systems-theoretical model, but it does offer an articulated example of how performance, adaptivity and underdetermination may intersect.

In this sense, the investigated domain illustrates a broader problem: how to approach systems that function reliably without fitting completely within a single explanatory framework. The findings presented here can therefore be read as both a conclusion and an opening. They conclude the specific empirical investigation, but open a broader reflection on the relationship between behaviour, model and understanding — a reflection that extends beyond the study of homing pigeons to other domains in which performance is compelling while explanations necessarily remain plural.

II. Exploration

The tension described above between robust performance and persistent explanatory pluralism is not confined to biological navigational systems. A comparable architectural constellation is found in contemporary artificial learning systems, particularly systems that function through large-scale exposure to heterogeneous datasets and statistical adjustment of weights within extremely high-dimensional parameter structures.

These systems are not constructed around a single explanatory principle, but develop their functioning through iterative adaptation based on large-scale variation. In their most extensive form, they operate on the basis of what may be designated as the 'ALL': the collection of all textual, visual and symbolic data available in digital form and integrated into training procedures. Its comprehensiveness means that it is not one collection among others, but a structural totality of available digital variation from which the system derives statistical regularities.

The performance of such systems can be remarkably stable and adaptive. At the same time, their internal configuration proves difficult to reduce to a single exclusive explanatory scheme that is both complete and necessary. Attempts at explainability commonly result in multiple mutually compatible reconstructions of internal functioning, without any one reconstruction being justifiably regarded as definitive.

The tension between functioning and explanation identified in the biological domain appears here once again, although within a different material and technical context. The analogy with the system investigated in this dissertation therefore concerns not similarity of mechanism, but similarity of architecture.

In both biological and artificial systems, robust behaviour depends on redundancy, distributed representation and adaptive reweighting of signals under continuous exposure to variation. In both cases, stable output can be observed while different explanatory frameworks remain compatible with the observed behaviour. Reduction to a single necessary explanatory axis cannot be compelled through analysis of output alone. Internal organisation can be reconstructed only indirectly, and that reconstruction remains plural in a particular sense.

This suggests that underdetermination in such systems should not simply be understood as a temporary consequence of limited knowledge, but may be related to their architectural construction. Where redundancy and large-scale variation are structurally embedded, robustness arises not despite plurality, but because of it. Resistance to explanation may then constitute a secondary effect of the way in which stability is generated.

This has implications for the design of future artificial systems. Where robust performance arises from architectural pluralism and large-scale integration of the ALL, the demand for complete internal transparency may conflict with adaptive capacity. This does not render explainability unnecessary, but it may mean that explainability cannot be achieved through complete reduction to a single explanatory line. Alternative forms of characterisation may be required in which multiple compatible descriptions can coexist without this being treated as epistemological failure.

Viewed in this light, the study of homing pigeons provides no normative programme for artificial intelligence, but it does provide an empirically articulated example of a type of system in which performance, redundancy and explanatory pluralism occur simultaneously. It shows that the relationship between functioning and understanding is not necessarily linear. Where comparable tensions arise in systems operating on the basis of the ALL, they may be interpreted less as anomalies than as structural consequences of a particular form of architecture.

III. Internal Representation versus Retrospective Reconstruction

A more precise formulation of this parallel requires a distinction that often remains implicit in discussions of both biological and artificial systems, but is epistemologically crucial: the distinction between reconstruction and representation.

When a system functions robustly, it is tempting to assume that it contains an internally coherent and reconstructable model that fully explains this functioning. In many cases, however, scientific explanation rests on retrospective reconstruction: an analytical reordering of observed behaviour in terms of theoretical categories intelligible to the researcher. Such a reconstructive model need not coincide with the internal representational structure actually employed by the system.

In the biological system investigated here, this meant that multiple assumption structures remained compatible with stable behavioural outcomes. The explanations formulated — for example, in terms of cue integration, hierarchical prioritisation or adaptive reweighting — function as interpretative frameworks that render behaviour coherent. They are methodologically necessary, but their necessity for the operation of the system itself cannot simply be assumed. Behaviour may remain stable without being internally organised according to a single explicitly reconstructable logic.

A comparable tension arises in artificial systems trained on the basis of the AL. When such systems produce consistent and semantically compelling output, there is a tendency to describe their functioning in terms of implicit knowledge structures or latent models. Subsequent explanations — for example, in terms of vector spaces, activation patterns or weight distributions — are attempts to reconstruct internal states in language intelligible to humans.

Here too, however, these reconstructions need not coincide with the manner in which the system 'organises' itself. Its internal representation is distributed, high-dimensional and not primarily designed for transparency. The explanation is an external projection, not a readable blueprint from within.

The distinction between reconstruction and representation clarifies why underdetermination cannot simply be regarded as an epistemological deficiency. Where multiple reconstructions are consistent with observed performance, this need not mean that one of them fails to capture the 'true' internal organisation. It may instead mean that the internal organisation does not correspond unambiguously to a single human-interpretable model.

In systems centred on redundancy and large-scale exposure to variation, functioning may arise from statistical stability and reciprocal compensation without these processes being reducible to a single hierarchically ordered representation.

This insight has implications for how knowledge of such systems is understood. Where robust performance can be generated without a transparent, coherent and exclusive underlying model, intelligibility is not a precondition for functioning, but a separate epistemological layer. Scientific explanation is then not a direct window onto internal logic, but an approach that structures behaviour in intelligible terms. It is necessary for intersubjective communication and testing, but need not be identical to the operational architecture of the system itself.

In light of the preceding analysis, underdetermination can be reconsidered as a possible structural consequence of system architectures built on redundancy, adaptive reweighting and integration of the AL. Where such architectures predominate, stability arises not through reduction to a single explanatory axis, but through interaction among multiple contributions that partially overlap and compensate for one another. Explanation and functioning then operate at different levels.

This dissertation has made that tension visible within a natural-scientific framework. Its implications nevertheless extend further, without therefore requiring less precise formulation.

IV. Final clarification.

A final methodological clarification concerns the production of this dissertation. The text and empirical configurations were developed through iterative interaction with an artificial language system, under the author's complete substantive selection, organisation and final responsibility. The data presented in the preceding chapters were constructed or generated within the research design described and function as an analytical instrument for systematically exploring the limits of explanatory reduction.

This method of production is not separate from the central subject of the research. On the contrary, the manner in which the dissertation was produced itself illustrates the relationship between architecture, performance and explanatory transparency investigated throughout this study.

References.

Angelaki, D. E., Gu, Y., & DeAngelis, G. C. (2009). Multisensory integration: Psychophysics, neurophysiology, and computation. *Current Opinion in Neurobiology, 19*(4), 452–458.

Ashby, F. G., & Maddox, W. T. (2005). Human category learning. *Annual Review of Psychology, 56*, 149–178.

Berg, M. E., et al. (2011). Categorization of multidimensional stimuli by pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 37*(3), 331–344.

Biro, D., Guilford, T., Dell'Omo, G., & Lipp, H.-P. (2004). Familiar route loyalty implies visual pilotage in homing pigeons. *Proceedings of the National Academy of Sciences, 101*(50), 17440–17443.

Blough, D. S. (1975). Steady-state generalization and discrimination in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 1*, 3–15.

Cheng, K., & Spetch, M. L. (2011). Mechanisms of landmark use in mammals and birds. In E. A. Wasserman & T. R. Zentall (Eds.), *The Oxford handbook of comparative cognition*. Oxford University Press.

Cook, R. G. (Ed.). (2001). *Avian visual cognition*. Comparative Cognition Press.

Cook, R. G., Katz, J. S., & Cavoto, B. R. (1997). Pigeon perception and discrimination of complex visual stimuli. *Journal of Experimental Psychology: Animal Behavior Processes, 23*, 123–143.

Directive 2010/63/EU of the European Parliament and of the Council of 22 September 2010 on the protection of animals used for scientific purposes.

Edwards, C. A. (1987). Feature selection and categorization in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 13*(1), 39–47.

Ernst, M. O., & Bülthoff, H. H. (2004). Merging the senses into a robust percept. *Trends in Cognitive Sciences, 8*(4), 162–169.

European Commission. (2020). *Working document on the implementation of Directive 2010/63/EU on the protection of animals used for scientific purposes*.

Fetsch, C. R., Pouget, A., DeAngelis, G. C., & Angelaki, D. E. (2012). Neural correlates of reliability-based cue weighting during multisensory integration. *Nature Neuroscience, 15*(1), 146–154.

Gagliardo, A. (2013). Forty years of olfactory navigation in birds. *Journal of Experimental Biology, 216*, 2165–2171.

Gagliardo, A., et al. (2009). Homing in pigeons: The role of visual landmarks revisited. *Journal of Experimental Biology, 212*, 353–362.

Gigerenzer, G., & Selten, R. (Eds.). (2001). *Bounded rationality: The adaptive toolbox*. MIT Press.

Gigerenzer, G., Todd, P. M., & the ABC Research Group. (1999). *Simple heuristics that make us smart*. Oxford University Press.

Guilford, T., & Biro, D. (2014). Route-following and landmark-based navigation in pigeons. *Philosophical Transactions of the Royal Society B, 369*(1635), 20130048.

Hempel, C. G. (1965). *Aspects of scientific explanation and other essays in the philosophy of science*. Free Press.

Herrnstein, R. J., Loveland, D. H., & Cable, C. (1976). Natural concepts in pigeons. *Journal of Experimental Psychology: Animal Behavior Processes, 2*(4), 285–302.

Honig, W. K., & Stewart, K. E. (1988). Pigeons can discriminate locations presented in pictures. *Journal of the Experimental Analysis of Behavior, 50*, 215–231.

Jacobs, L. F., & Schenk, F. (2003). Unpacking the cognitive map: The parallel map theory of hippocampal function. *Psychological Review, 110*(2), 285–315.

Kitano, H. (2004). Biological robustness. *Nature Reviews Genetics, 5*, 826–837.

Kramer, G. (1953). Wird die Sonnenhöhe bei der Heimfindeorientierung verwertet? *Journal für Ornithologie, 94*, 201–219.

Kramer, G. (1953). Orientation of birds by the sun. *Nature, 172*, 417–419.

Laudan, L. (1977). *Progress and its problems: Toward a theory of scientific growth*. University of California Press.

Lazareva, O. F., & Wasserman, E. A. (2012). Categories and concepts in animals. In E. A. Wasserman & T. R. Zentall (Eds.), *The Oxford handbook of comparative cognition*. Oxford University Press.

Lea, S. E. G., & Ryan, C. M. E. (1990). Feature analysis of pigeons' acquisition of concept discrimination. *Journal of Experimental Psychology: Animal Behavior Processes, 16*, 132–143.

Mayo, D. G. (2018). *Statistical inference as severe testing*. Cambridge University Press.

Mayr, E. (1982). *The growth of biological thought: Diversity, evolution, and inheritance*. Harvard University Press.

Mouritsen, H. (2018). Long-distance navigation and magnetoreception in migratory animals. *Nature, 558*, 50–59.

Nosofsky, R. M. (1986). Attention, similarity, and the identification–categorization relationship. *Journal of Experimental Psychology: General, 115*, 39–57.

Nosofsky, R. M. (1992). Exemplars, prototypes, and similarity rules. In A. F. Healy, S. M. Kosslyn, & R. M. Shiffrin (Eds.), *From learning theory to connectionist theory*. Erlbaum.

Pearce, J. M. (1994). Similarity and discrimination: A selective review and a connectionist model. *Psychological Review, 101*, 587–607.

Papi, F., Fiore, L., Fiaschi, V., & Benvenuti, S. (1972). Olfaction and homing in pigeons. *Monitore Zoologico Italiano, 6*, 85–95.

Reed, S. K. (1972). Pattern recognition and categorization. *Cognitive Psychology, 3*, 382–407.

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature, 413*, 591–596.

Simon, H. A. (1956). Rational choice and the structure of the environment. *Psychological Review, 63*(2), 129–138.

Smith, J. D., & Minda, J. P. (2000). Thirty categorization results in search of a model. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 26*, 3–27.

Stanford, P. K. (2006). *Exceeding our grasp: Science, history, and the problem of unconceived alternatives*. Oxford University Press.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie, 20*, 410–433.

Turner, B. M., & Wasserman, E. A. (2023). Learning complex category structures. *Psychonomic Bulletin & Review, 30*, 1–19.

Wallraff, H. G. (2005). *Avian navigation: Pigeon homing as a paradigm*. Springer.

Wasserman, E. A., et al. (2014). Parallel acquisition of multiple categories by pigeons. *Journal of Experimental Psychology: Animal Learning and Cognition, 40*(3), 267–277.

Watanabe, S. (1993). Object–picture equivalence in the pigeon. *Behavioural Processes, 30*, 1–13.

Weisberg, M. (2007). Three kinds of idealization. *The Journal of Philosophy, 104*(12), 639–659.

Wiltschko, R., & Wiltschko, W. (1972). Magnetic compass of European robins. *Science, 176*, 62–64.

Wiltschko, R., & Wiltschko, W. (2005). Magnetic orientation and magnetoreception in birds. *Journal of Experimental Biology, 208*, 2589–2599

Appendix A: Raw Data for Chapter 5

(Dataset: 30 pigeons × 5 conditions = 150 test flights.)

Explanatory Note to Appendix A – Raw Dataset for RQ2 (Homing under Variation in Individual Cues).

This appendix contains the complete raw dataset on which the analyses in Chapter 5 are based. Thirty homing pigeons each completed the control condition and the four conditions involving manipulation of an individual cue once. The dataset therefore comprises 150 test flights: thirty paired observations per condition.

A.1 Coding and observation window. All pigeons eventually returned to the home loft. Episodes with Return = 0 concern arrivals outside the predefined observation window of 240 minutes. No return time within the analytical window is reported for these episodes; they remain included in the dataset for calculating timely return.

A.2 Performance variables**.** The following were recorded for each test flight: Episode ID, date, Pigeon ID, condition code, release distance, wind force, availability of the four navigational cues, timely return, return time, initial orientation deviation and route index. Each Pigeon ID occurs once within each of the five conditions. The biological sample therefore comprises thirty pigeons; the 150 rows are paired observations, not 150 independent animals.

A.3 Distance design and data checks. Each condition contains exactly six test flights at each of five release distances (86, 88, 90, 92 and 94 km). The distance range within each condition is therefore 86–94 km and the mean distance is always 90 km. The distribution is rotated across Pigeon IDs and test dates; at least eleven days separate two flights by the same pigeon. For ease of verification, the table is ordered by condition code and Pigeon ID, while the dates reflect the randomised order of execution. Within all five conditions, release distance and return time are positively associated among timely returns. These checks serve solely to assess the internal consistency of the synthetic dataset.

Episode ID	Date	Pigeon ID	Condition	Distance (km)	Wind (Bft)	Mag.	Olf.	Sun	Vis.	Timely	Time (min)	Deviation (°)	Route index
E001	2025-09-01	D1	C0	86	2	1	1	1	1	1	65.6	13.4	0.870
E002	2025-09-01	D2	C0	86	2	1	1	1	1	1	65.9	12.5	0.866
E003	2025-09-01	D3	C0	86	2	1	1	1	1	1	65.2	6.8	0.881
E004	2025-09-01	D4	C0	86	2	1	1	1	1	1	65.9	9.2	0.881
E005	2025-09-01	D5	C0	86	2	1	1	1	1	1	66.1	10.0	0.864
E006	2025-09-01	D6	C0	86	2	1	1	1	1	1	68.0	11.1	0.863
E007	2025-09-26	D7	C0	88	3	1	1	1	1	1	69.2	11.1	0.859
E008	2025-09-26	D8	C0	88	3	1	1	1	1	1	69.1	14.2	0.859
E009	2025-09-26	D9	C0	88	3	1	1	1	1	1	68.4	9.4	0.868
E010	2025-09-26	D10	C0	88	3	1	1	1	1	1	71.9	12.9	0.860
E011	2025-09-26	D11	C0	88	3	1	1	1	1	1	68.2	9.1	0.881
E012	2025-09-26	D12	C0	88	3	1	1	1	1	1	69.0	12.6	0.870
E013	2025-10-22	D13	C0	90	4	1	1	1	1	1	72.2	12.2	0.859
E014	2025-10-22	D14	C0	90	4	1	1	1	1	1	71.8	11.1	0.862
E015	2025-10-22	D15	C0	90	4	1	1	1	1	1	72.4	10.1	0.876
E016	2025-10-22	D16	C0	90	4	1	1	1	1	1	72.9	10.2	0.868
E017	2025-10-22	D17	C0	90	4	1	1	1	1	1	74.4	15.8	0.849
E018	2025-10-22	D18	C0	90	4	1	1	1	1	1	72.6	15.6	0.849
E019	2025-09-19	D19	C0	92	3	1	1	1	1	1	71.4	13.1	0.855
E020	2025-09-19	D20	C0	92	3	1	1	1	1	1	72.4	9.9	0.872
E021	2025-09-19	D21	C0	92	3	1	1	1	1	1	73.4	13.9	0.868
E022	2025-09-19	D22	C0	92	3	1	1	1	1	1	73.8	12.4	0.861
E023	2025-09-19	D23	C0	92	3	1	1	1	1	1	70.1	6.5	0.886
E024	2025-09-19	D24	C0	92	3	1	1	1	1	1	71.6	9.4	0.867
E025	2025-10-15	D25	C0	94	4	1	1	1	1	1	75.1	11.1	0.862
E026	2025-10-15	D26	C0	94	4	1	1	1	1	1	73.0	10.8	0.870
E027	2025-10-15	D27	C0	94	4	1	1	1	1	1	74.3	9.1	0.871
E028	2025-10-15	D28	C0	94	4	1	1	1	1	1	72.0	7.1	0.880
E029	2025-10-15	D29	C0	94	4	1	1	1	1	1	75.3	15.6	0.848
E030	2025-10-15	D30	C0	94	4	1	1	1	1	1	76.3	13.9	0.853
E031	2025-10-06	D1	C1	88	2	0	1	1	1	1	70.7	18.0	0.831
E032	2025-10-06	D2	C1	88	2	0	1	1	1	1	70.0	16.7	0.837
E033	2025-10-06	D3	C1	88	2	0	1	1	1	1	70.6	16.8	0.839
E034	2025-10-06	D4	C1	88	2	0	1	1	1	1	69.7	11.2	0.853
E035	2025-10-06	D5	C1	88	2	0	1	1	1	1	70.9	15.7	0.830
E036	2025-10-06	D6	C1	88	2	0	1	1	1	1	73.2	14.5	0.825

Episode ID	Date	Pigeon ID	Condition	Distance (km)	Wind (Bft)	Mag.	Olf.	Sun	Vis.	Timely	Time (min)	Deviation (°)	Route index
E037	2025-09-03	D7	C1	90	4	0	1	1	1	1	73.5	13.3	0.833
E038	2025-09-03	D8	C1	90	4	0	1	1	1	1	73.7	14.8	0.827
E039	2025-09-03	D9	C1	90	4	0	1	1	1	1	72.2	17.1	0.824
E040	2025-09-03	D10	C1	90	4	0	1	1	1	1	76.1	17.7	0.822
E041	2025-09-03	D11	C1	90	4	0	1	1	1	1	76.8	18.4	0.807
E042	2025-09-03	D12	C1	90	4	0	1	1	1	1	75.4	18.4	0.817
E043	2025-09-29	D13	C1	92	2	0	1	1	1	1	72.6	13.8	0.837
E044	2025-09-29	D14	C1	92	2	0	1	1	1	1	76.0	14.7	0.832
E045	2025-09-29	D15	C1	92	2	0	1	1	1	1	80.0	21.0	0.813
E046	2025-09-29	D16	C1	92	2	0	1	1	1	1	77.4	16.7	0.827
E047	2025-09-29	D17	C1	92	2	0	1	1	1	1	79.4	17.6	0.812
E048	2025-09-29	D18	C1	92	2	0	1	1	1	1	73.9	13.6	0.840
E049	2025-10-24	D19	C1	94	3	0	1	1	1	1	74.7	14.4	0.833
E050	2025-10-24	D20	C1	94	3	0	1	1	1	1	77.5	14.9	0.833
E051	2025-10-24	D21	C1	94	3	0	1	1	1	1	78.3	17.2	0.824
E052	2025-10-24	D22	C1	94	3	0	1	1	1	1	79.2	16.8	0.815
E053	2025-10-24	D23	C1	94	3	0	1	1	1	0		37.8	0.690
E054	2025-10-24	D24	C1	94	3	0	1	1	1	1	75.2	14.7	0.842
E055	2025-09-22	D25	C1	86	2	0	1	1	1	1	70.9	14.6	0.834
E056	2025-09-22	D26	C1	86	2	0	1	1	1	1	70.9	16.3	0.826
E057	2025-09-22	D27	C1	86	2	0	1	1	1	1	70.5	14.9	0.829
E058	2025-09-22	D28	C1	86	2	0	1	1	1	1	68.5	17.1	0.835
E059	2025-09-22	D29	C1	86	2	0	1	1	1	1	69.6	15.9	0.825
E060	2025-09-22	D30	C1	86	2	0	1	1	1	1	72.2	18.6	0.820
E061	2025-09-12	D1	C2	90	3	1	0	1	1	1	79.9	29.5	0.755
E062	2025-09-12	D2	C2	90	3	1	0	1	1	1	82.6	34.0	0.744
E063	2025-09-12	D3	C2	90	3	1	0	1	1	1	80.5	28.5	0.753
E064	2025-09-12	D4	C2	90	3	1	0	1	1	0		52.2	0.617
E065	2025-09-12	D5	C2	90	3	1	0	1	1	1	79.2	26.0	0.760
E066	2025-09-12	D6	C2	90	3	1	0	1	1	1	80.9	27.3	0.759
E067	2025-10-08	D7	C2	92	4	1	0	1	1	1	85.5	31.5	0.740
E068	2025-10-08	D8	C2	92	4	1	0	1	1	1	87.7	36.4	0.719
E069	2025-10-08	D9	C2	92	4	1	0	1	1	1	79.9	23.0	0.771
E070	2025-10-08	D10	C2	92	4	1	0	1	1	1	88.1	31.6	0.742
E071	2025-10-08	D11	C2	92	4	1	0	1	1	1	85.7	31.0	0.740
E072	2025-10-08	D12	C2	92	4	1	0	1	1	0		51.1	0.622

Episode ID	Date	Pigeon ID	Condition	Distance (km)	Wind (Bft)	Mag.	Olf.	Sun	Vis.	Timely	Time (min)	Deviation (°)	Route index
E073	2025-09-05	D13	C2	94	3	1	0	1	1	1	84.6	29.8	0.748
E074	2025-09-05	D14	C2	94	3	1	0	1	1	1	86.0	31.8	0.746
E075	2025-09-05	D15	C2	94	3	1	0	1	1	1	87.9	26.0	0.753
E076	2025-09-05	D16	C2	94	3	1	0	1	1	1	87.6	30.1	0.745
E077	2025-09-05	D17	C2	94	3	1	0	1	1	1	86.9	29.1	0.760
E078	2025-09-05	D18	C2	94	3	1	0	1	1	1	86.8	33.1	0.741
E079	2025-10-01	D19	C2	86	4	1	0	1	1	1	75.6	30.4	0.755
E080	2025-10-01	D20	C2	86	4	1	0	1	1	1	79.2	28.6	0.756
E081	2025-10-01	D21	C2	86	4	1	0	1	1	0		43.0	0.636
E082	2025-10-01	D22	C2	86	4	1	0	1	1	1	78.3	26.7	0.756
E083	2025-10-01	D23	C2	86	4	1	0	1	1	1	76.5	25.7	0.761
E084	2025-10-01	D24	C2	86	4	1	0	1	1	1	76.4	24.0	0.765
E085	2025-10-27	D25	C2	88	2	1	0	1	1	1	79.6	26.5	0.763
E086	2025-10-27	D26	C2	88	2	1	0	1	1	1	77.7	26.9	0.760
E087	2025-10-27	D27	C2	88	2	1	0	1	1	1	77.2	26.0	0.767
E088	2025-10-27	D28	C2	88	2	1	0	1	1	1	78.3	25.9	0.753
E089	2025-10-27	D29	C2	88	2	1	0	1	1	1	81.2	35.4	0.736
E090	2025-10-27	D30	C2	88	2	1	0	1	1	1	81.1	29.9	0.748
E091	2025-10-17	D1	C3	92	3	1	1	0	1	1	76.3	20.4	0.797
E092	2025-10-17	D2	C3	92	3	1	1	0	1	1	76.2	16.9	0.810
E093	2025-10-17	D3	C3	92	3	1	1	0	1	1	76.2	18.2	0.810
E094	2025-10-17	D4	C3	92	3	1	1	0	1	1	79.6	20.7	0.798
E095	2025-10-17	D5	C3	92	3	1	1	0	1	1	76.7	18.9	0.805
E096	2025-10-17	D6	C3	92	3	1	1	0	1	1	81.0	24.1	0.783
E097	2025-09-15	D7	C3	94	2	1	1	0	1	0		39.8	0.670
E098	2025-09-15	D8	C3	94	2	1	1	0	1	1	81.6	23.2	0.780
E099	2025-09-15	D9	C3	94	2	1	1	0	1	1	79.0	20.0	0.800
E100	2025-09-15	D10	C3	94	2	1	1	0	1	1	81.7	20.9	0.793
E101	2025-09-15	D11	C3	94	2	1	1	0	1	1	77.5	13.3	0.818
E102	2025-09-15	D12	C3	94	2	1	1	0	1	1	78.4	20.7	0.804
E103	2025-10-10	D13	C3	86	3	1	1	0	1	1	72.0	20.9	0.808
E104	2025-10-10	D14	C3	86	3	1	1	0	1	1	73.7	22.2	0.793
E105	2025-10-10	D15	C3	86	3	1	1	0	1	1	73.4	18.3	0.807
E106	2025-10-10	D16	C3	86	3	1	1	0	1	1	76.4	23.4	0.790
E107	2025-10-10	D17	C3	86	3	1	1	0	1	1	76.5	24.4	0.789
E108	2025-10-10	D18	C3	86	3	1	1	0	1	1	74.3	22.1	0.792

Episode ID	Date	Pigeon ID	Condition	Distance (km)	Wind (Bft)	Mag.	Olf.	Sun	Vis.	Timely	Time (min)	Deviation (°)	Route index
E109	2025-09-08	D19	C3	88	2	1	1	0	1	1	74.1	23.3	0.789
E110	2025-09-08	D20	C3	88	2	1	1	0	1	1	75.0	19.4	0.801
E111	2025-09-08	D21	C3	88	2	1	1	0	1	1	76.5	25.1	0.785
E112	2025-09-08	D22	C3	88	2	1	1	0	1	1	77.4	22.9	0.775
E113	2025-09-08	D23	C3	88	2	1	1	0	1	1	75.1	17.0	0.799
E114	2025-09-08	D24	C3	88	2	1	1	0	1	1	75.0	21.6	0.794
E115	2025-10-03	D25	C3	90	3	1	1	0	1	1	77.9	19.8	0.802
E116	2025-10-03	D26	C3	90	3	1	1	0	1	0		40.5	0.655
E117	2025-10-03	D27	C3	90	3	1	1	0	1	1	75.2	16.8	0.812
E118	2025-10-03	D28	C3	90	3	1	1	0	1	1	76.3	20.7	0.796
E119	2025-10-03	D29	C3	90	3	1	1	0	1	1	77.5	23.7	0.785
E120	2025-10-03	D30	C3	90	3	1	1	0	1	1	81.1	25.1	0.779
E121	2025-09-24	D1	C4	94	4	1	1	1	0	1	80.8	24.4	0.781
E122	2025-09-24	D2	C4	94	4	1	1	1	0	1	82.4	25.5	0.772
E123	2025-09-24	D3	C4	94	4	1	1	1	0	0		43.4	0.647
E124	2025-09-24	D4	C4	94	4	1	1	1	0	1	84.0	26.1	0.770
E125	2025-09-24	D5	C4	94	4	1	1	1	0	1	81.7	22.2	0.780
E126	2025-09-24	D6	C4	94	4	1	1	1	0	1	81.8	23.1	0.784
E127	2025-10-20	D7	C4	86	2	1	1	1	0	1	76.3	24.0	0.769
E128	2025-10-20	D8	C4	86	2	1	1	1	0	1	77.9	28.9	0.746
E129	2025-10-20	D9	C4	86	2	1	1	1	0	1	73.1	23.9	0.773
E130	2025-10-20	D10	C4	86	2	1	1	1	0	1	75.6	23.2	0.784
E131	2025-10-20	D11	C4	86	2	1	1	1	0	1	77.6	23.8	0.766
E132	2025-10-20	D12	C4	86	2	1	1	1	0	1	74.2	26.0	0.779
E133	2025-09-17	D13	C4	88	4	1	1	1	0	1	77.6	25.3	0.767
E134	2025-09-17	D14	C4	88	4	1	1	1	0	0		47.0	0.624
E135	2025-09-17	D15	C4	88	4	1	1	1	0	1	79.0	23.6	0.780
E136	2025-09-17	D16	C4	88	4	1	1	1	0	1	81.5	27.4	0.763
E137	2025-09-17	D17	C4	88	4	1	1	1	0	1	78.8	23.6	0.774
E138	2025-09-17	D18	C4	88	4	1	1	1	0	1	78.6	25.5	0.769
E139	2025-10-13	D19	C4	90	2	1	1	1	0	1	77.2	25.7	0.767
E140	2025-10-13	D20	C4	90	2	1	1	1	0	1	79.9	26.0	0.768
E141	2025-10-13	D21	C4	90	2	1	1	1	0	1	81.3	29.2	0.765
E142	2025-10-13	D22	C4	90	2	1	1	1	0	1	80.4	29.3	0.762
E143	2025-10-13	D23	C4	90	2	1	1	1	0	1	78.5	22.3	0.777
E144	2025-10-13	D24	C4	90	2	1	1	1	0	1	79.7	25.9	0.765

Episode ID	Date	Pigeon ID	Condition	Distance (km)	Wind (Bft)	Mag.	Olf.	Sun	Vis.	Timely	Time (min)	Deviation (°)	Route index
E145	2025-09-10	D25	C4	92	4	1	1	1	0	1	82.4	23.3	0.780
E146	2025-09-10	D26	C4	92	4	1	1	1	0	1	81.6	24.9	0.767
E147	2025-09-10	D27	C4	92	4	1	1	1	0	0		51.6	0.624
E148	2025-09-10	D28	C4	92	4	1	1	1	0	1	80.7	24.1	0.771
E149	2025-09-10	D29	C4	92	4	1	1	1	0	1	79.9	24.2	0.774
E150	2025-09-10	D30	C4	92	4	1	1	1	0	1	83.0	24.2	0.770

Appendix B: Raw Data for Chapter 6

(Dataset: 30 pigeons × 5 conditions = 150 test flights.)

Explanatory Note to Appendix B – Raw Dataset for RQ3 (Homing under Cumulative Variation).

This appendix contains the complete raw dataset on which the analyses in Chapter 6 are based. The same thirty homing pigeons as in Chapter 5 each completed the five configurations involving combined cue reduction once. The dataset therefore comprises 150 test flights: five paired observations per pigeon. The biological sample is N = 30; the 150 rows do not represent 150 independent animals.

B.1 Coding and observation window. All pigeons eventually returned to the home loft. Episodes with Timely = 0 concern arrivals outside the predefined observation window of 240 minutes. No return time within the analytical window is reported for these episodes; they remain fully included for calculating timely return. No fictitious return time of 240 minutes is assigned.

B.2 Configurations and performance variables. C5 to C8 are two-cue reductions (D2); C9 is a three-cue reduction (D3). A value of 1 indicates availability without experimental manipulation and a value of 0 indicates the standardised reduction. The following were recorded for each test flight: Episode ID, date, Pigeon ID, condition and reduction level, release distance, wind force, cue configuration, timely return, return time, initial orientation deviation and route index. The Episode ID continues from Appendix A and runs from E151 to E300.

B.3 Distance design and order of execution. Each configuration contains exactly six test flights at each of five release distances (86, 88, 90, 92 and 94 km). The mean release distance is therefore always 90 km. Each pigeon flies each distance once and completes each configuration once. At least eleven days separate two flights by the same pigeon. For ease of verification, the table is ordered by condition code and Pigeon ID; the dates reflect the counterbalanced order of execution.

B.4 Data checks against C0. The control condition in Appendix A shows 100.0% timely return, a mean return time of 70.9 minutes, a mean route index of 0.866 and a mean initial deviation of 11.3°. For D2, these values are 92.5%, 87.8 minutes, 0.691 and 35.0°, respectively; for D3, they are 86.7%, 100.9 minutes, 0.597 and 51.6°. The ordering C0 > D2 > D3 is therefore present across all four performance indicators. Within each configuration, release distance and return time are positively associated among timely returns; the derived mean route speed varies only slightly. These checks serve solely to assess the internal consistency of the synthetic dataset.

Episode ID	Date	Pigeon ID	Cond./level	Distance (km)	Wind (Bft)	Mag.	Olf.	Sun	Vis.	Timely	Time (min)	Deviation (°)	Route index
E151	2025-11-03	D1	C5/D2	86	2	0	0	1	1	1	81.2	33.3	0.705
E152	2025-11-03	D2	C5/D2	86	2	0	0	1	1	1	82.0	32.3	0.697
E153	2025-11-03	D3	C5/D2	86	2	0	0	1	1	1	83.1	34.3	0.690
E154	2025-11-03	D4	C5/D2	86	2	0	0	1	1	0		48.1	0.597
E155	2025-11-03	D5	C5/D2	86	2	0	0	1	1	1	80.3	31.0	0.712
E156	2025-11-03	D6	C5/D2	86	2	0	0	1	1	1	83.4	27.7	0.706
E157	2025-11-28	D7	C5/D2	88	3	0	0	1	1	1	86.2	34.9	0.694
E158	2025-11-28	D8	C5/D2	88	3	0	0	1	1	1	85.3	36.9	0.695
E159	2025-11-28	D9	C5/D2	88	3	0	0	1	1	1	83.1	33.1	0.712
E160	2025-11-28	D10	C5/D2	88	3	0	0	1	1	1	87.7	34.5	0.696
E161	2025-11-28	D11	C5/D2	88	3	0	0	1	1	1	84.8	31.1	0.715
E162	2025-11-28	D12	C5/D2	88	3	0	0	1	1	0		51.9	0.590
E163	2025-12-24	D13	C5/D2	90	4	0	0	1	1	1	87.3	29.6	0.705
E164	2025-12-24	D14	C5/D2	90	4	0	0	1	1	1	90.8	37.7	0.694
E165	2025-12-24	D15	C5/D2	90	4	0	0	1	1	1	90.7	30.3	0.701
E166	2025-12-24	D16	C5/D2	90	4	0	0	1	1	1	90.6	32.2	0.696
E167	2025-12-24	D17	C5/D2	90	4	0	0	1	1	1	90.1	31.6	0.696
E168	2025-12-24	D18	C5/D2	90	4	0	0	1	1	1	88.5	31.7	0.701
E169	2025-11-21	D19	C5/D2	92	3	0	0	1	1	1	85.7	32.1	0.710
E170	2025-11-21	D20	C5/D2	92	3	0	0	1	1	1	89.8	32.1	0.708
E171	2025-11-21	D21	C5/D2	92	3	0	0	1	1	0		52.7	0.595
E172	2025-11-21	D22	C5/D2	92	3	0	0	1	1	1	91.2	33.8	0.693
E173	2025-11-21	D23	C5/D2	92	3	0	0	1	1	1	90.0	33.6	0.695
E174	2025-11-21	D24	C5/D2	92	3	0	0	1	1	1	88.5	31.6	0.702
E175	2025-12-17	D25	C5/D2	94	4	0	0	1	1	1	94.1	32.9	0.700
E176	2025-12-17	D26	C5/D2	94	4	0	0	1	1	1	92.0	32.1	0.699
E177	2025-12-17	D27	C5/D2	94	4	0	0	1	1	1	91.1	35.8	0.703
E178	2025-12-17	D28	C5/D2	94	4	0	0	1	1	1	90.5	31.6	0.704
E179	2025-12-17	D29	C5/D2	94	4	0	0	1	1	1	92.5	34.0	0.691
E180	2025-12-17	D30	C5/D2	94	4	0	0	1	1	1	93.2	35.1	0.700
E181	2025-12-08	D1	C6/D2	88	2	0	1	0	1	1	79.3	28.1	0.742
E182	2025-12-08	D2	C6/D2	88	2	0	1	0	1	1	78.3	28.4	0.749
E183	2025-12-08	D3	C6/D2	88	2	0	1	0	1	1	79.0	28.2	0.743
E184	2025-12-08	D4	C6/D2	88	2	0	1	0	1	1	81.8	31.8	0.731
E185	2025-12-08	D5	C6/D2	88	2	0	1	0	1	1	78.9	22.3	0.745
E186	2025-12-08	D6	C6/D2	88	2	0	1	0	1	1	80.0	28.0	0.742

Episode ID	Date	Pigeon ID	Cond./level	Distance (km)	Wind (Bft)	Mag.	Olf.	Sun	Vis.	Timely	Time (min)	Deviation (°)	Route index
E187	2025-11-05	D7	C6/D2	90	4	0	1	0	1	1	84.2	28.3	0.728
E188	2025-11-05	D8	C6/D2	90	4	0	1	0	1	1	84.3	30.2	0.731
E189	2025-11-05	D9	C6/D2	90	4	0	1	0	1	1	81.8	25.8	0.743
E190	2025-11-05	D10	C6/D2	90	4	0	1	0	1	1	85.1	27.0	0.741
E191	2025-11-05	D11	C6/D2	90	4	0	1	0	1	1	83.7	25.6	0.749
E192	2025-11-05	D12	C6/D2	90	4	0	1	0	1	1	84.4	28.7	0.728
E193	2025-12-01	D13	C6/D2	92	2	0	1	0	1	1	82.7	23.8	0.744
E194	2025-12-01	D14	C6/D2	92	2	0	1	0	1	1	85.7	29.8	0.723
E195	2025-12-01	D15	C6/D2	92	2	0	1	0	1	1	86.3	26.2	0.748
E196	2025-12-01	D16	C6/D2	92	2	0	1	0	1	1	87.2	28.9	0.740
E197	2025-12-01	D17	C6/D2	92	2	0	1	0	1	1	86.5	27.1	0.744
E198	2025-12-01	D18	C6/D2	92	2	0	1	0	1	1	83.4	28.2	0.745
E199	2025-12-26	D19	C6/D2	94	3	0	1	0	1	1	84.6	27.7	0.744
E200	2025-12-26	D20	C6/D2	94	3	0	1	0	1	1	85.6	25.2	0.752
E201	2025-12-26	D21	C6/D2	94	3	0	1	0	1	1	89.3	28.2	0.726
E202	2025-12-26	D22	C6/D2	94	3	0	1	0	1	1	86.5	28.7	0.742
E203	2025-12-26	D23	C6/D2	94	3	0	1	0	1	0		44.0	0.632
E204	2025-12-26	D24	C6/D2	94	3	0	1	0	1	1	85.7	25.0	0.741
E205	2025-11-24	D25	C6/D2	86	2	0	1	0	1	1	79.0	26.7	0.752
E206	2025-11-24	D26	C6/D2	86	2	0	1	0	1	1	77.6	31.5	0.742
E207	2025-11-24	D27	C6/D2	86	2	0	1	0	1	1	79.0	30.1	0.741
E208	2025-11-24	D28	C6/D2	86	2	0	1	0	1	1	77.4	24.4	0.747
E209	2025-11-24	D29	C6/D2	86	2	0	1	0	1	1	78.3	28.7	0.741
E210	2025-11-24	D30	C6/D2	86	2	0	1	0	1	1	80.3	26.0	0.732
E211	2025-11-14	D1	C7/D2	90	3	1	0	0	1	1	87.9	40.0	0.676
E212	2025-11-14	D2	C7/D2	90	3	1	0	0	1	1	88.9	41.0	0.677
E213	2025-11-14	D3	C7/D2	90	3	1	0	0	1	0		60.0	0.556
E214	2025-11-14	D4	C7/D2	90	3	1	0	0	1	1	92.2	40.0	0.664
E215	2025-11-14	D5	C7/D2	90	3	1	0	0	1	1	91.0	36.5	0.669
E216	2025-11-14	D6	C7/D2	90	3	1	0	0	1	1	91.1	39.0	0.671
E217	2025-12-10	D7	C7/D2	92	4	1	0	0	1	1	95.7	41.5	0.664
E218	2025-12-10	D8	C7/D2	92	4	1	0	0	1	1	92.3	44.4	0.673
E219	2025-12-10	D9	C7/D2	92	4	1	0	0	1	1	92.4	35.3	0.665
E220	2025-12-10	D10	C7/D2	92	4	1	0	0	1	1	96.3	40.1	0.668
E221	2025-12-10	D11	C7/D2	92	4	1	0	0	1	1	95.2	39.0	0.673
E222	2025-12-10	D12	C7/D2	92	4	1	0	0	1	1	94.8	45.9	0.661

Episode ID	Date	Pigeon ID	Cond./level	Distance (km)	Wind (Bft)	Mag.	Olf.	Sun	Vis.	Timely	Time (min)	Deviation (°)	Route index
E223	2025-11-07	D13	C7/D2	94	3	1	0	0	1	1	96.1	39.8	0.667
E224	2025-11-07	D14	C7/D2	94	3	1	0	0	1	0		55.4	0.555
E225	2025-11-07	D15	C7/D2	94	3	1	0	0	1	1	98.6	37.7	0.666
E226	2025-11-07	D16	C7/D2	94	3	1	0	0	1	1	99.5	39.2	0.662
E227	2025-11-07	D17	C7/D2	94	3	1	0	0	1	1	100.6	39.6	0.658
E228	2025-11-07	D18	C7/D2	94	3	1	0	0	1	1	97.5	40.0	0.658
E229	2025-12-03	D19	C7/D2	86	4	1	0	0	1	1	85.2	38.8	0.666
E230	2025-12-03	D20	C7/D2	86	4	1	0	0	1	1	89.6	40.8	0.666
E231	2025-12-03	D21	C7/D2	86	4	1	0	0	1	1	91.2	43.3	0.650
E232	2025-12-03	D22	C7/D2	86	4	1	0	0	1	1	88.9	38.4	0.666
E233	2025-12-03	D23	C7/D2	86	4	1	0	0	1	1	87.8	39.1	0.665
E234	2025-12-03	D24	C7/D2	86	4	1	0	0	1	1	86.1	38.8	0.673
E235	2025-12-29	D25	C7/D2	88	2	1	0	0	1	1	88.3	39.6	0.673
E236	2025-12-29	D26	C7/D2	88	2	1	0	0	1	1	89.2	43.3	0.661
E237	2025-12-29	D27	C7/D2	88	2	1	0	0	1	0		60.8	0.561
E238	2025-12-29	D28	C7/D2	88	2	1	0	0	1	1	88.0	40.0	0.670
E239	2025-12-29	D29	C7/D2	88	2	1	0	0	1	1	89.1	38.5	0.664
E240	2025-12-29	D30	C7/D2	88	2	1	0	0	1	1	93.2	39.7	0.655
E241	2025-12-19	D1	C8/D2	92	3	1	1	0	0	1	88.4	32.3	0.695
E242	2025-12-19	D2	C8/D2	92	3	1	1	0	0	1	88.1	32.6	0.702
E243	2025-12-19	D3	C8/D2	92	3	1	1	0	0	1	90.8	35.8	0.679
E244	2025-12-19	D4	C8/D2	92	3	1	1	0	0	1	92.4	37.7	0.683
E245	2025-12-19	D5	C8/D2	92	3	1	1	0	0	1	89.1	32.8	0.687
E246	2025-12-19	D6	C8/D2	92	3	1	1	0	0	1	90.4	33.5	0.694
E247	2025-11-17	D7	C8/D2	94	2	1	1	0	0	0		53.3	0.583
E248	2025-11-17	D8	C8/D2	94	2	1	1	0	0	1	93.2	37.3	0.682
E249	2025-11-17	D9	C8/D2	94	2	1	1	0	0	1	90.3	31.2	0.697
E250	2025-11-17	D10	C8/D2	94	2	1	1	0	0	1	95.8	31.8	0.687
E251	2025-11-17	D11	C8/D2	94	2	1	1	0	0	1	91.6	29.1	0.704
E252	2025-11-17	D12	C8/D2	94	2	1	1	0	0	1	93.0	35.1	0.682
E253	2025-12-12	D13	C8/D2	86	3	1	1	0	0	1	84.3	30.9	0.693
E254	2025-12-12	D14	C8/D2	86	3	1	1	0	0	1	86.2	35.0	0.680
E255	2025-12-12	D15	C8/D2	86	3	1	1	0	0	1	89.2	34.8	0.683
E256	2025-12-12	D16	C8/D2	86	3	1	1	0	0	1	87.9	35.9	0.691
E257	2025-12-12	D17	C8/D2	86	3	1	1	0	0	1	88.8	34.4	0.683
E258	2025-12-12	D18	C8/D2	86	3	1	1	0	0	1	85.0	34.5	0.685

Episode ID	Date	Pigeon ID	Cond./level	Distance (km)	Wind (Bft)	Mag.	Olf.	Sun	Vis.	Timely	Time (min)	Deviation (°)	Route index
E259	2025-11-10	D19	C8/D2	88	2	1	1	0	0	1	83.2	33.2	0.692
E260	2025-11-10	D20	C8/D2	88	2	1	1	0	0	1	87.4	36.1	0.691
E261	2025-11-10	D21	C8/D2	88	2	1	1	0	0	1	89.9	36.2	0.668
E262	2025-11-10	D22	C8/D2	88	2	1	1	0	0	1	87.2	34.4	0.692
E263	2025-11-10	D23	C8/D2	88	2	1	1	0	0	1	86.7	33.6	0.690
E264	2025-11-10	D24	C8/D2	88	2	1	1	0	0	1	85.5	33.8	0.693
E265	2025-12-05	D25	C8/D2	90	3	1	1	0	0	1	88.7	29.5	0.701
E266	2025-12-05	D26	C8/D2	90	3	1	1	0	0	0		54.6	0.586
E267	2025-12-05	D27	C8/D2	90	3	1	1	0	0	1	90.5	34.5	0.672
E268	2025-12-05	D28	C8/D2	90	3	1	1	0	0	1	86.8	32.8	0.696
E269	2025-12-05	D29	C8/D2	90	3	1	1	0	0	1	88.3	35.7	0.689
E270	2025-12-05	D30	C8/D2	90	3	1	1	0	0	1	89.2	35.5	0.693
E271	2025-11-26	D1	C9/D3	94	4	0	0	0	1	1	102.2	47.4	0.616
E272	2025-11-26	D2	C9/D3	94	4	0	0	0	1	1	104.7	48.7	0.612
E273	2025-11-26	D3	C9/D3	94	4	0	0	0	1	1	106.1	48.2	0.603
E274	2025-11-26	D4	C9/D3	94	4	0	0	0	1	1	106.5	52.6	0.600
E275	2025-11-26	D5	C9/D3	94	4	0	0	0	1	1	103.3	45.9	0.615
E276	2025-11-26	D6	C9/D3	94	4	0	0	0	1	1	104.5	49.3	0.617
E277	2025-12-22	D7	C9/D3	86	2	0	0	0	1	0		71.8	0.508
E278	2025-12-22	D8	C9/D3	86	2	0	0	0	1	1	94.4	52.0	0.612
E279	2025-12-22	D9	C9/D3	86	2	0	0	0	1	1	92.1	45.4	0.626
E280	2025-12-22	D10	C9/D3	86	2	0	0	0	1	1	97.5	48.6	0.611
E281	2025-12-22	D11	C9/D3	86	2	0	0	0	1	1	96.7	48.2	0.609
E282	2025-12-22	D12	C9/D3	86	2	0	0	0	1	0		70.4	0.503
E283	2025-11-19	D13	C9/D3	88	4	0	0	0	1	1	97.3	47.1	0.611
E284	2025-11-19	D14	C9/D3	88	4	0	0	0	1	0		68.0	0.506
E285	2025-11-19	D15	C9/D3	88	4	0	0	0	1	1	102.2	50.1	0.607
E286	2025-11-19	D16	C9/D3	88	4	0	0	0	1	1	100.5	48.8	0.617
E287	2025-11-19	D17	C9/D3	88	4	0	0	0	1	1	101.2	49.0	0.612
E288	2025-11-19	D18	C9/D3	88	4	0	0	0	1	1	98.7	51.1	0.606
E289	2025-12-15	D19	C9/D3	90	2	0	0	0	1	1	98.5	46.4	0.603
E290	2025-12-15	D20	C9/D3	90	2	0	0	0	1	1	99.5	47.4	0.615
E291	2025-12-15	D21	C9/D3	90	2	0	0	0	1	0		71.2	0.502
E292	2025-12-15	D22	C9/D3	90	2	0	0	0	1	1	100.1	46.4	0.613
E293	2025-12-15	D23	C9/D3	90	2	0	0	0	1	1	100.9	50.7	0.600
E294	2025-12-15	D24	C9/D3	90	2	0	0	0	1	1	96.0	47.6	0.626

Episode ID	Date	Pigeon ID	Cond./level	Distance (km)	Wind (Bft)	Mag.	Olf.	Sun	Vis.	Timely	Time (min)	Deviation (°)	Route index
E295	2025-11-12	D25	C9/D3	92	4	0	0	0	1	1	102.8	44.0	0.622
E296	2025-11-12	D26	C9/D3	92	4	0	0	0	1	1	104.2	51.8	0.604
E297	2025-11-12	D27	C9/D3	92	4	0	0	0	1	1	102.6	50.7	0.610
E298	2025-11-12	D28	C9/D3	92	4	0	0	0	1	1	99.7	47.9	0.620
E299	2025-11-12	D29	C9/D3	92	4	0	0	0	1	1	104.6	50.6	0.600
E300	2025-11-12	D30	C9/D3	92	4	0	0	0	1	1	105.6	49.9	0.609