Tactile senses and foraging in birds, with emphasis on kiwi

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Abstract

Probe-foraging birds must often rely on senses other than vision for prey-detection. One such sense is 'remote touch': the detection of vibration and pressure cues from prey within the substrate. Remote touch is mediated by the 'scolopacid-type bill-tip organ', which consists of a honeycomb of sensory pits in the bill-tip, containing clusters of mechanoreceptors. This organ was originally described in the neognathous shorebird family Scolopacidae, but was recently also discovered in paleognathous kiwi (Apterygidae): an example of convergent/parallel evolution. My aim was to discover how widespread this organ is among birds, compare its anatomy and function in foraging between kiwi and other probe-foraging birds and elucidate in detail the foraging behaviours and senses used by free-living kiwi. Within the thesis I compare the bill-tip organs of kiwi and shorebirds using material from the brown kiwi (Apterygidae: *Apteryx mantelli*) and bar-tailed godwit (Scolopacidae: *Limosa lapponica*). I provide the first description of the organ in a third family of birds, the ibises (Threskiornithidae), and give evidence that it may exist in simplified form in a fourth family, Rallidae. The Scolopacidae, Apterygidae, Threskiornithidae and Rallidae are widely separated on the avian phylogenetic tree. This suggests that the evolution of the scolopacid-type bill-tip organ and associated sense is favoured by a probe-foraging lifestyle. Foraging trials confirm the bill-tip organs of brown kiwi and Madagascar crested ibises (*Lophotibis cristata urschi*) are functional for remote touch. The ibises rely solely on remote touch to find buried prey, whereas brown kiwi use the sense in conjunction with olfaction. Free-living brown kiwi display no obviously visually-guided behaviours, instead using hearing (head-lifting in response to noises audible to the observer), olfaction (odour sensing behaviour, 'sniffing,' in the direction of these sounds) and touch. Kiwi tap ahead with their bill-tip when walking and move their facial bristles forward when foraging, forming a 'net' on the ground. The bristle follicles in kiwi (and some other insectivorous bird species) are innervated with Herbst corpuscles, suggesting tactile function. Female kiwi probe on average 30% deeper than males and juveniles, but there are no other differences in foraging behaviour between the sexes.

Acknowledgements

A PhD is the ‘long haul’ and sitting down to write the acknowledgements section for one is a daunting task. I have so very many people to thank that some of them will inevitably get left out. If that happens to be you: I apologise! I am deeply grateful for everyone’s input and if I accidentally forget to mention you through some horrible oversight, come and find me: I’ll buy you a beer instead (or a wine, if you’d prefer).

The fact that this PhD happened at all is the fault of Isabel Castro. I met Isa when I was 11 years old, after reading her article on face-to-face copulation in hihi in Forest & Bird. I wrote her a letter about her article and she invited me to help out with her post-doc on Mokoia Island, chasing hihi. I was so inspired by Isabel’s energy and passion for her subject that I decided I wanted to be a field biologist, too. When I was looking for a supervisor for post graduate studies, Isabel was the obvious choice. Isa: you have been more than a supervisor to me - you have been a friend and an inspiration for over half of my life. I’m not sure I can thank you enough!

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My family – you made me what I am (you might blame Rob Guest for the crazy bird thing, but you most certainly encouraged it!). Thank you for giving me everything, for believing in me, for supporting me through thick and thin. Mum – thank you for your faith in me and for being there always and getting me through the tough times. Dad, your pride in me drives me to achieve to the highest of my ability, thank you. Michele you're not only my favourite little big sister but also one of my best friends and a wonderful tramping companion! Alastair, you're the best big brother in the world, Agnes the most wonderful sister-in-law. Ken & Raylene, it's been a fantastic thing to know you're just down the road if ever I need you. Terry & Katya, thank you so much for your support and your love. All of you inspire me, I am so very lucky to have you as my family.

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Preface

This thesis contains six chapters and two appendices, plus a general Introduction and Discussion. Data from Chapter 1 are included in two separate publications, one already published, the other still in preparation. Chapters 2 – 6 and Appendix 2 each constitute a single published, or in press paper, Appendix 1 has been submitted to the New Zealand Journal of Ecology. Chapters are presented in the order in which they were submitted for publication, except for Chapter 1 which was completed last. All the data presented here are new, and each chapter builds upon those written before it. Therefore, there is extensive cross-referencing between chapters. Chapters have been reformatted for consistency within the thesis.

This is a thesis by papers, and each paper also stands alone. Therefore, there is inevitably some repetition of material between chapters, particularly in some of the topics covered in the introductions, and in the methods sections.

Authorship of papers arising from Chapters 1 – 6, Appendix 1

I am the first author in all published, in press or submitted papers arising from Chapters 1 – 6 and Appendix 1 of this thesis. In all cases my input into the paper was the greatest in terms of development of ideas, synthesis of experiment design, collection and analysis of data, and drafting of each manuscript. Below, I give the references for the publications arising from each chapter of the thesis and elucidate the roles of the co-authors on those publications. Isabel Castro was my chief PhD supervisor and Murray Potter and Maurice Alley co-supervised. Therefore, each of these people additionally supported the writing of each paper within their supervisory roles.

Chapter 1:

This chapter contains information on the bill-tip morphology of five kiwi species published in the *Journal of Anatomy*, where it appears in conjunction with data from my BSc (Hons). In this thesis I only present the data which I collected as part of my PhD,

after I completed my BSc (Hons). It also contains data on the kiwi and godwit bill-tip organs which will be submitted within a manuscript to *Brain, Behaviour and Evolution*, together with information on kiwi and godwit brains collected by Jeremy Corfield (data on the brains are not presented here).

Chapter references: Cunningham, S., Castro, I., and Alley, M. 2007. A new prey-detection mechanism for kiwi (*Apteryx* spp.) suggests convergent evolution between paleognathous and neognathous birds. Journal of Anatomy. 211 (4): 493-502.

Cunningham, S.J. and Corfield, J. Comparative anatomy of the trigeminal system in a kiwi and a shorebird *in prep.*

Contributions of co-authors: Isabel Castro was heavily involved in conception of ideas and planning for fieldwork and in discussions of kiwi bill-tip histology, for the *Journal of Anatomy* paper. She also commented on chapter drafts. Maurice Alley initially taught me to interpret histology slides during my BSc (Hons) and contributed to the interpretation of histological material presented in the *Journal of Anatomy* paper. He also kindly discussed with me the interpretation of the histology of kiwi Herbst corpuscles presented within this chapter (particularly the three-dimensional shape of the central axon, and the density of the outer zone), and commented on chapter drafts. Jeremy Corfield collected and analysed data on kiwi and godwit brain morphology for the *Brain, Behaviour and Evolution* paper, which is not presented in this chapter. He also acted as a liaison with the micro-CT technician at Auckland University when I sent kiwi and godwit beak samples up for scanning, and taught me how to construct three dimensional models from µCT scans using the image analysis software package AMIRA™.

Chapter 2:

This chapter appears exactly as published in *Animal Behaviour* (except for the replacement of ‘kiwis’ with the more correct plural, ‘kiwi’).

Chapter reference: Cunningham, S.J., Castro, I. & Potter, M.A. 2009. The relative importance of olfaction and remote touch in prey detection by North Island brown kiwis. Animal Behaviour 78: 899-905.

Contributions of co-authors: Isabel Castro contributed ideas on experimental design for this paper. She carried out behaviour trials with kiwi at San Diego Zoo while I was across town working with kiwi at San Diego Wild Animal Park. Unfortunately, husbandry management practices for kiwi at the Zoo and Park meant we were unable to control trial conditions sufficiently. The data from these trials are therefore not included in this chapter or in the paper. Isabel also spent considerable time helping to improve the wording of the results section. Murray Potter contributed ideas on experimental design for this paper. Both co-authors commented on manuscript drafts.

Chapter 3:

This chapter appears exactly as published in *The Auk.*

Chapter reference: Cunningham, S.J., Alley, M.R., Castro, I., Potter, M.A., Cunningham M.J., Pyne M.J. In press. Bill morphology of ibises suggests a remote-tactile sensory system for prey detection. Auk.

Contributions of co-authors: Maurice Alley was involved in sourcing an ibis specimen for histology via veterinarian Michael Pyne at Currumbin Wildlife Sanctuary, Australia. He also discussed interpretation of histology slides, and the trend in bill-morphology with habitat use with me. Isabel Castro and Murray Potter discussed the trend in bill-morphology with habitat use with me and provided advice on the inclusion of some of the ideas in the discussion section. Malcolm Cunningham discussed at length the physics of sound wave travel in various substrates with me, and contributed to ideas presented within the discussion section. Mic Pyne (veterinarian, Currumbin Wildife Sanctuary) euthanized the ibis used for histology, and undertook initial sample preparation (fixing the head and bill in formalin). He provided extensive help organising import and export permits to bring the ibis head to New Zealand. Maurice, Isabel, Murray and Malcolm all commented on paper drafts.

Chapter 4:

Chapter reference: Cunningham, S. J., Castro, I., Jensen, T. and Potter, M. A. Remote touch prey-detection by Madagascar Crested Ibises. *Submitted to the Journal of Avian Biology.*

Contributions of co-authors: Isabel Castro contributed ideas on experimental design for this paper. She assisted me with training ibises at San Diego Zoo and Wild Animal Park, and with carrying out the trials. Tom Jensen assisted me with training ibises at San Diego Zoo and Wild Animal Park, with carrying out the trials, and with sourcing equipment and organising permission to undertake work with these birds. Murray Potter contributed ideas on experimental design for this paper. All co-authors also commented on paper drafts.

Chapter 5:

Chapter reference: Cunningham, S. J. and Castro, I. The secret life of wild brown kiwi: direct foraging observations and other nocturnal behaviours. *Submitted to the New Zealand Journal of Ecology.*

Contributions of co-authors: Isabel Castro helped to collect some of the video footage used in this paper, provided advice on manuscript structure, and commented on drafts.

Chapter 6:

Chapter reference: Cunningham, S. J., Alley, M., and Castro, I. Facial bristle structure and function in insectivorous birds in New Zealand. *Submitted to the Journal of Morphology.*

Contributions of co-authors: Maurice Alley contributed to early discussions of ideas for this paper, provided advice on the writing of the results, and ideas on the functional significance of structural differences between Herbst corpuscles. Isabel Castro contributed to early discussions of ideas for this paper. Both co-authors commented on manuscript drafts.

Appendix 1:

Appendix reference: Cunningham, S.J. and Castro, I. Short term effects of leg-mounted radio-transmitters in brown kiwi. *Formatted for the New Zealand Journal of Ecology*.

Contributions of co-authors: Isabel Castro provided and analysed data on behaviour of kiwi on exiting burrows, and provided photographs of leg injuries and entanglement caused by transmitters. She also commented on manuscript drafts.

Data on injuries to kiwi caused by transmitters was collected by the whole kiwi research team on Ponui Island during successive catch weeks. These data were compiled by Isabel, and analysed by me for this paper.

Authorship of Appendix 2

I am the second author of the paper presented in Appendix 2. This paper arose from an ongoing study of olfaction in wild kiwi which is related to the topics of this thesis, and in which I continue to have a part. The majority of data analysis, synthesis of ideas, and drafting of the paper were carried out by the first author, Isabel Castro. Below I set out my contribution to this paper.

Appendix reference: Castro, I., Cunningham, S.J., Gsell, A.C., Jaffe, K., Cabrera, A., Liendo, C. *In press.* Olfaction in birds: A closer look at the Kiwi (Apterygidae). Journal of Avian Biology.

My contribution: I was involved in initial and ongoing discussions with co-authors (particularly Isabel Castro and Anna Gsell) regarding ideas for this point-of-view paper. I collected (but did not analyse) the majority of the field data used in the paper, during the course of video-recording for Chapter 5 and Appendix 1 of this thesis, and during training experiments to assess whether behaviour trials from Chapter 2 could also be run in the wild (we did not achieve this). The drawings for Figure 1 were done by me, using still frames from video-recordings I collected. I commented on the paper drafts. I was not involved in the laboratory work for this paper, nor in collecting or analysing papers for the extensive literature review. The ‘author contributions’ section at the end of Appendix 2 acknowledges the roles of the other authors on this paper.

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Susan Cunningham, PhD candidate	Dr. Isabel Castro, chief supervisor

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