

1 **Olfaction in birds: A closer look at the Kiwi (Apterygidae)**

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14 Here we present a historical summary of our present knowledge on avian olfaction
15 followed by a more detailed overview of olfaction in North Island brown kiwi
16 (*Apteryx mantelli*). The article argues in favour of the importance of bird olfaction
17 using evidence from the literature as well as our own observations.

18

19 **Olfaction in birds**

20 The evidence concerning the olfactory capability of birds and thus its potential use in
21 their every day life is now overwhelming. Overtime however, it has been the source
22 of much disagreement. In the early days of research into avian olfaction, the “small
23 size” of most avian olfactory bulbs was taken as evidence that this sense was
24 unimportant (Hill 1905; reviewed in Strong 1911). However, Strong (1911) dissected
25 the olfactory organs of 65 species of birds (27 orders) and concluded that based on
26 their size, the sense of smell could not be considered non-functional. One hundred
27 years (mid 19th to mid 20th century) of behavioural observations and poorly designed
28 experiments on a handful of bird species produced contradictory and confusing results
29 which failed to elucidate a possible use of olfaction by birds (e.g. earlier papers
30 reviewed by Strong 1911, including Audubon 1826; Darwin 1901; and Benham 1906;
31 later work including: Meek 1922; Williams 1922; Soudek 1927; Marples 1931;
32 Walter 1943; Hamrun 1953).

33

34 The first controlled experiments to test the function of the olfactory system in birds
35 were carried out by Michelsen (1959) and showed that pigeons were able to learn
36 food discrimination using odours as cues. A great deal of work on the anatomy and

37 physiology of the olfactory apparatus and olfactory capabilities of birds followed this
38 finding. Bang (1960) presented a description and photographs of the well developed
39 olfactory apparatus of turkey vultures (*Cathartes aurea*), Trinidad oilbirds (*Steatornis*
40 *caripensis*), Laysan (*Diomedea immutabilis*), and blackfooted albatrosses (*D.*
41 *nigripes*), offering behavioural observations to support the use of olfaction by each
42 species. She followed this with a more detailed and extensive document in 1971
43 examining the anatomy of the olfactory system of avian species in 23 orders and
44 providing evidence that olfaction should be a functioning sense in birds (Bang 1971).
45 In 1968, Bang and Cobb reviewed the studies on olfactory bulb size and the
46 comparative studies of the nasal fossa of birds, showing enormous variation between
47 different groups of birds in these measurements.

48

49 Tucker (1965) and Wenzel (1965) measured the electrophysiological response of the
50 olfactory tissue of several species of birds when stimulated by odorants, concluding
51 that all birds tested had a physiologically functional olfactory apparatus. Further
52 extensive electrophysiological and behavioural work with more bird species continued
53 to support this result (most of this work was done by Wenzel et al. but also Roper et
54 al.; reviewed in Roper 1999).

55

56 Electrophysiological and anatomical work firmly established the functionality of the
57 olfactory system in birds. However, the degree of olfactory sensitivity remained
58 unknown. To date, olfactory thresholds have only been measured in a few species of
59 birds. Results show that the birds' range of sensitivity to odours is similar to values
60 obtained for mammals such as rats and rabbits (Stattleman et al. 1975; Snyder and

61 Peterson 1979; Smith and Paselk 1986; Walker et al. 1986; reviewed in Waldvogel
62 1989 and Clark et al. 1993). In more recent times, researchers have searched the avian
63 genome for the presence and extent of olfactory receptor (OR) genes (Gray and Hurst
64 1998; Leibovici et al. 1996; Nef et al. 1996; Niimura and Nei 2005; Steiger et al.
65 2008; Steiger et al. 2009a) which are associated to odorant detection in vertebrates.
66 The most recent research shows that the number of OR genes in 9 species of birds
67 correlates with the size of the olfactory bulb (Steiger et al. 2008). Furthermore, the
68 sizes of the OR genes in kiwi (*A. australis*), kakapo (*Strigops habroptilus*) and jungle
69 fowl (*Gallus gallus*), resemble those of mammalian genomes (Steiger et al. 2008).
70 More interestingly, although the size of the olfactory bulb and the number of OR
71 genes in the starling are small (Steiger et al. 2008), this species is able to discriminate
72 odours and use olfaction to select specific herbs (Gwinner and Berger 2008).

73

74 Experimental behavioural studies regarding the use of olfaction in birds have found
75 that several species of procellariiformes (e.g. work by Bang et al., Wenzel et al.,
76 Benvenuti et al., Bonadonna et al., and others; and reviewed in: Waldvogel 1989;
77 Roper 1999 and Nevitt 2008); pigeons (research mainly by Papi et al; Wallraff et al.;
78 Wiltschko et al; Benvenuti et al.; and reviewed in Papi 1990; Wiltschko 1996;
79 Wallraff 2003; more recently: Mora et al. 2004; Gagliardo et al. 2007; Jorge et al.
80 2009); and starlings (Wallraff et al. 1995) use olfaction in navigation and/or long
81 distance prey finding (reviews in: Papi 1990; Wallraff 2003; Rajchard 2008). Holland
82 et al. (2009) have recently provided evidence that catbirds (*Dumetella carolinensis*)
83 may use the olfactory sense in migratory orientation. Kiwi have been shown to be
84 able to find food at a shorter distance using the sense of olfaction alone or in
85 combination with remote touch (Wenzel 1968; Cunningham et al. 2009). Olfaction

86 has also been suggested, and in some cases found, to be implicated in defence, either
87 by deterring predators (Weldon and Rappole 1997; Dumbacher and Pruett Jones 1996;
88 Weldon 2000) or parasites (Weldon 2000; Petit et al. 2002; Douglas 2004, 2008), or
89 by making birds aware of possible poisons (Marples and Roper 1996; Skelhorn and
90 Rowe 2006), and in predator recognition (Amo et al. 2008).

91

92 The use of odours in avian social communication has also received recent
93 consideration (reviewed by Hagelin 2007; Hagelin and Jones 2007; Balthazart and
94 Taziaux 2009). For example, several species of birds, mostly procellariids but also
95 chickens (*Gallus domesticus*), have been found to respond to the smell of their
96 partner or other conspecifics (reviews above plus: Bonadonna et al. 2007; Jouventin et
97 al. 2007; Mardon and Bonadonna 2009); and others have been found to be able to
98 recognise their burrow as well as their own odour (reviews above plus: Smith and
99 Conway 2007; Mennerat 2008; O'Dwyer et al. 2008; Mardon and Bonadonna 2009).
100 In a recent experiment Whittaker et al. (2009) found that incubating female juncos
101 (*Junco hyemalis*) reduce incubation bout length in response to heterospecific's preen
102 gland secretion suggesting that odour may affect parental care.

103

104 **The kiwi**

105 Kiwi (*Apteryx* spp.) are ideal candidates for studying the use of olfaction in birds
106 because we already know that they have a highly developed and functional olfactory
107 system (Bang and Cobb 1968; Wenzel 1968, 1971; Bang 1971). It is also known that
108 kiwi use olfaction to find food (Wenzel 1968; Cunningham et al. 2009). In recent

109 years there has been an increase in our knowledge of kiwi brain anatomy and senses.
110 For example, Martin et al. (2007) found that kiwi have reduced eye sight and visual
111 field topography which are reflected in the small area of their brain associated with
112 this function. In contrast, the areas of the brain concerned with touch, olfaction
113 (Martin et al. 2007) and cognition (Corfield et al. 2008; Corfield 2009) are highly
114 developed. Cunningham et al. (2009) found that kiwi use a tactile sense called remote
115 touch to find food, in addition to, or in combination with smell. Steiger et al. (2009b)
116 have recently found that kiwi have a large number of OR genes and that those genes
117 are correlated with nocturnality. Corfield (2009) has been studying the auditory
118 capabilities and associated brain areas in kiwi, finding that kiwi have high frequency
119 specialisations similar to that of barn owls (*Tito alba*). Kiwi are nocturnal, ground
120 dwelling and forest species and therefore it makes sense for them to primarily use
121 senses other than vision in their every day lives.

122

123 It is our belief that the olfactory and tactile senses of kiwi are likely to be used for
124 more than one purpose (e.g. not just for foraging), due to their high degree of
125 development. Some evidence in support of this idea comes from the work of Jenkins
126 (2001). She examined, in an uncontrolled situation, the reactions of captive North
127 Island brown kiwi (here referred to as kiwi, *Apteryx mantelli*) to self and unfamiliar
128 kiwi faecal odour. She found behavioural responses ranging from attraction, to
129 avoidance and escape, which suggested a territorial use of faecal scent marks. Further
130 support for this idea comes from our field observations of wild kiwi. We used
131 motion-picture recording to video at least 30 wild kiwi in their natural environment.
132 Kiwi were interested and performed behaviours which we associate with olfactory

133 search, aimed towards research equipment, and towards other kiwi and people that
134 were outside their burrows or nearby while foraging.

135

136 Kiwi olfactory behaviours are reminiscent of mammalian sniffing. Individuals inhale
137 air noisily through the nostrils, with an exaggerated lifting of the beak, pointing the
138 bill several times in the direction of interest and moving the bill in a small arc in the
139 air (Figure 1)ⁱ. Similar behaviours have been reported for procellarid species (e.g.
140 DeBose and Nevitt 2008; O'Dwyer et al. 2008). For example, Leach's storm petrel
141 chicks (*Oceanodroma leucorhoa*) presented with odour choices sweep their heads in
142 broad arches around their body while making coughing noises and rapid biting
143 movements close to the source of odour (O'Dwyer et al. 2008). Our observations of
144 wild kiwi suggest that olfaction is used in conjunction with hearing (at longer
145 distances) and touch (at close proximity). For example, if an observer made a noise,
146 the observed bird would lift its head and then perform the olfactory search behaviour.
147 In some instances kiwi approached objects and people and touched them with their
148 beak. Kiwi have their nostrils at the end of their beak, a unique characteristic among
149 birds, and getting close to the objects may allow a better understanding of the source
150 of odour (or taste or chemosense), which would otherwise be hampered by the very
151 long bill. The bill-tip organ of kiwi (Cunningham et al. 2007) together with the sense
152 of olfaction/taste may interact to allow kiwi to build a mental picture of the object and
153 its location.

154

155 The loud inhaling associated with olfaction in kiwi may be a mechanism used to
156 transport fluids containing the odour back to the olfactory concha in the upper reaches

157 of the bill (Bang 1971). The loudness of the inhaling may reflect the effort necessary
158 to transport the scent of interest, particularly if there is urgency to determine the
159 source/composition of the smell. For example, female beaks may reach 12 cm in
160 length in Great Spotted kiwi (*Apteryx haastii*) and some populations of brown kiwi
161 (Sales 2005). Kiwi also make a snorting sound with unknown function. In our videos,
162 snorting was associated with both foraging and olfactory search. Wenzel (1971)
163 suggested that snorting functions to clear the nostrils after probing or tapping. We
164 suggest that snorting in the context of olfactory search has an additional function.
165 Kiwi produce abundant nasal secretions which are often visible when the birds are
166 caught as they 'blow bubbles' through their nostrils. We associate this 'bubble
167 blowing' with handling stress (Wenzel 1971; authors' pers. obs.) because 'bubble
168 blowing' has never been observed in the wild. However, we have video recorded
169 instances of sniffing or snorting wild kiwi sounding as if they had fluid in the nasal
170 chamber. We think that the production of nasal drip together with the loud sniffing
171 and snorting could be a way to aid the spread of nasal drip, in which the odours could
172 be dissolved, from the nasal glands at the top of the bill to the nostrils and back. We
173 suggest that nasal secretion should be produced more abundantly when the bird
174 actively 'sniffs' particularly if the scent source is far from the bird or during stressful
175 situations.

176

177 **Use of olfaction in kiwi social interactions**

178 The observations described above suggest that kiwi may be using olfaction to gather
179 information about other organisms in their environment, for example predators or
180 competitors, and conspecifics. Like petrels, kiwi emanate a notably unusual odour

181 which Buller (1888) referred to as “a peculiar earthy smell”. Kiwi faeces also have a
182 strongly pungent smell that incorporates this ‘earthy’ body scent with the smell of
183 ammonia (authors’ pers. obs.). Using gas chromatography Antarctic prion (*Pachyptila*
184 *desolata*) feathers have been recently found to have individual chemical profiles
185 (Bonadonna et al. 2007). We hypothesise that kiwi odours, like those of petrels, may
186 be specific to individual kiwi, providing an opportunity for social communication.

187

188 To examine this possibility, we undertook a preliminary examination of the chemical
189 composition of kiwi faeces to determine the presence of substances which may
190 provide faeces with their characteristic scent and which may allow kiwi to leave
191 chemical messages. Kiwi faeces were collected in our study site in 2004 and 2006,
192 stored in glass vials and frozen at -20°C. We extracted volatiles from five faeces using
193 hexane, dichloromethane and methanol. Extracts were examined by gas
194 chromatography and mass spectrophotometry and compounds were identified by
195 interpretation of mass spectra, comparison to database library and/or using retention
196 data from authentic standards.

197

198 The chemical compounds found in kiwi excreta (Table 1) were common hexane
199 soluble hydrocarbons of the kind previously described by Jacob (1982) from
200 secretions of the kiwi uropygial gland and which are found in sebaceous glands and
201 most pheromone secreting glands in other animals. Wild kiwi faeces are often found
202 in conspicuous places such as on logs and roots (J. Miles pers. comm.; authors’ pers.
203 obs.), on tracks (authors’ pers. obs.), and also are accumulated inside some burrows
204 (J. Miles, pers. comm.; authors’ pers. obs.). Kiwi may be depositing information-

205 loaded faeces in key locations where conspecifics may encounter them to provide
206 information about breeding condition, burrow occupancy, or activity, as many
207 mammals (e.g. reviewed in Johnson 1973; Goszczynski 1990; Feldman 1994; Ralls
208 and Smith 2004; Barja et al. 2005) and reptiles do (e.g. Horne and Jaeger 1988; Bull
209 *et al.* 1999; Carpenter and Duvall, 1995).

210

211 The similarity between the compounds in faeces with those found in the uropygial
212 gland secretion examined by Jacob (1982) led us to begin investigating the uropygial
213 gland of kiwi as a source of scents. Pycraft (1910) and Paris (1913; in Jacob and
214 Ziswiler 1982) suggested that the uropygial gland of birds was a scent gland because
215 many of the constituents of the waxes produced in the glands are very odorous.

216 Uropygial gland secretions are typically preened through the feathers in most bird
217 species, distributing their compounds all over their body and potentially spreading a
218 chemical message on the bird's feathers which could be interpreted by conspecifics.

219 The composition of the uropygial gland in female mallard ducks (*Anas platyrhynchos*)
220 varies dramatically during the breeding season. The main change is caused by the
221 production of pheromones (Kolattukudy and Rogers 1987) which were found to be
222 influenced by sex hormones (Bohnet et al. 1991; Hiremath et al. 1992). Using gas
223 chromatography Jacob (1982) found the same type of compounds which are
224 precursors of the pheromones present in female mallards during the breeding season,
225 in the uropygial gland secretion from kiwi. We are currently examining the
226 composition of individual kiwi preen gland secretions to determine whether there are
227 differences and if these are also associated with sex and season.

228

229 The kiwi uropygial gland is very large and located adjacent to the cloaca (Beddard
230 1899; Figure 2). The location of the uropygial gland leads us to hypothesise that
231 chemicals may be produced in the gland and then deposited on the faeces to be used
232 as social markers. This hypothesis remains to be tested. Although the uropygial gland
233 is an obvious candidate for the production of scented markers, we cannot exclude the
234 possibility that anal glands, also located in close proximity to the birds' cloaca (Coil
235 and Wetherbee, 1959), are not involved.

236

237 Kiwi characteristic body odour could also be produced in at least two other type of
238 glands that could manufacture scented products which could be used in chemical
239 communication: the entire skin of many birds contains numerous cells capable of
240 sebaceous secretions (Lucas and Stettenheim, 1972; Menon and Menon, 2000;
241 Stettenheim 2000); and the external ear sebaceous glands (Lucas and Stettenheim,
242 1972). In addition, Douglas (2008) has recently described the production of fragrant
243 aldehydes, used for alloanointing by crested auklets (*Aethia cristatella*), by secretory
244 wick feathers.

245

246 **Concluding remarks**

247 We consider there is enough evidence that birds can use olfaction and that some
248 species do so regularly; it is now important to determine to what extent this sense is
249 used in the group Aves. In most of the studies above, the interest has been in how
250 individual species use the sense of olfaction for a particular purpose such as
251 navigation or foraging. It seems to us that the approach in these studies has generally

252 been to show that the sense of smell *alone* is used for a particular purpose. However,
253 the evidence suggests that birds use the sense of smell in conjunction with other
254 senses (Strong 1911; DeBose and Nevitt 2008). Experiments therefore should aim to
255 decipher the role of smell when used in combination to other senses (DeBose and
256 Nevitt 2008) and sometimes this will mean that new senses need to be discovered first
257 (e.g. Cunningham et al. 2007; Cunningham et al. 2009).

258

259 **Acknowledgements**

260 We thank the Chamberlin family for allowing our research on their land. Murray
261 Potter, Daniel Tompkins, Lee Shapiro, Julie Hagelin, Cleland Wallace, Barbara Helm
262 and several anonymous referees and the BEERS group at Massey Ecology provided
263 useful comments on earlier drafts of this paper. Thank you to Lee Shapiro, the Hojem
264 family especially Carryn, Ruth Elliot, Kyoko Mimura, Nikki Lydiard and David and
265 Amanda Scully for help obtaining footage of wild kiwi. Jonathan Miles provided
266 information and many hours of interesting conversations about kiwi which have been
267 fundamental to our investigations.

268 **Permits:** This project was carried out under New Zealand Department of
269 Conservation permits: AK/14971/RES; AK/20403/FAU and Massey University
270 Animal Ethics Approvals 06/91 and 06/105.

271 **Author contributions:** Conceived and designed ideas: IC, SC with contributions
272 from AG and KJ. Field Work: SC, IC, AG. Laboratory work: KJ, AC, CL. Wrote the
273 paper: IC with comments from all other authors and much advice from editors.

Table 1: Compounds found in Ponui Island brown kiwi *Apteryx mantelli* excreta after extraction with hexane, dichloromethane and methanol.

Compound
Phenol
Phenol-4-methyl
Benzenecarboxylic acid
Caprolactam
Cinnamaldehyde
Bicyclo(2,2,1)heptane-2-carboxylic acid 3,3-dimethyl
Decanoic acid
Tetradecane
alfa-Cubebene
Pentadecane
Butylated hydroxytoluene
Dodecanoic acid
Hexadecane
Pentadecane-2,6,10-dimethyl
Heptadecane
Tetradecanoic acid
Octadecane
16-octadecenal
Isopropyl myristate
Pentadecanoic acid
Nonadecane
9-hexadecenoic acid, methyl ester
Hexadecanoic acid, methyl ester
17-norkaur-15-ene, 13-methyl-(8beta, 13beta.)-
1,2-benzenedicarboxylic acid, butyl 2-methylpropyl ester
Eicosane
Octadecanal
Heptadecanoic acid
Kaur-16-ene
Heneicosane
9,12-octadecadienoic acid (Z,Z) methyl ester
9-octadecenoic acid, methyl ester
Octadecanoic acid, methyl ester
9,12 octadecadienoic acid (Z,Z)
Oleic acid
Octadecanoic acid
2-propenoic acid, 3-(4-methoxyphenyl)-,2-ethylhexyl ester
Docosane
3-tricosene
Ferruginol
Tetracosane
Pentacosane
Octacosane
Nonacosane
Triacontane
Hentriacontene
Cholestan-3-ol, (3beta,5beta)-
Cholest-5-en-3-ol (3beta)
Cholestan-3-ol
Ergosta-5,22-dien-3-ol
Ergosterol
Campesterol
Dotriacontane
Ergosta-5,8-dien-3-ol, (3.beta)
Sitosterol

Figure 1. Brown kiwi displaying olfactory search behaviour. Head is thrown up and back during each audible *sniff*. During olfactory search the bird assumes a stereotyped erect posture (central drawings). Drawings at either end show kiwi in alert (far left) and normal foraging postures (far right) with the head held below the level of the back. Disturbed kiwi often freeze in position (in this case mid-step) before displaying olfactory behaviour.

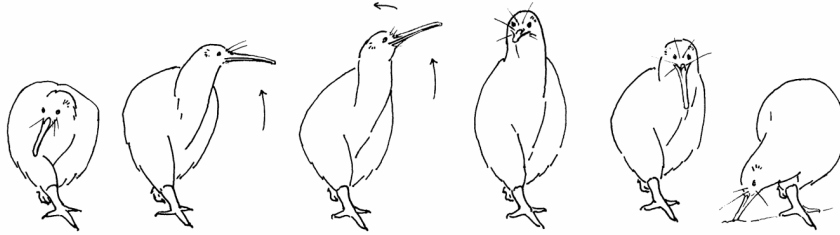


Figure 2. Brown kiwi uropygial gland. The head of the bird is located to the left of the photograph and the pygostyle to the right. C = Cloaca; U = Uropygial gland.



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ⁱ The 'sniffing' sound has been reported in the past by many (Buller 1888, Wenzel 1971; and many kiwi fieldworkers) in relation to foraging, but never in terms of other functions, and the behaviour associated with it has to our knowledge never been described.