

Bill trait variation in kākākāpō, *Strigops habroptilus* (Gray): differences between contemporary and historical birds

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Abstract Museum study-skins are an important though under-utilised resource for studying the biology of endangered birds. This study compares the bill and cere morphology of female and male kākākāpō (*Strigops habroptilus*) from three provenances: 1) “historical wild-origin” museum specimens collected from the North and South islands of New Zealand over 100 years ago; 2) the “modern wild-origin”, predominantly ex-Stewart Island Kākākāpō Recovery Programme (KRP) founder population; and 3) the “modern non-wild” descendants of the founder population raised and maintained under the conservation management of the KRP. Bill length and gape was found to be smaller in the historical wild-origin birds than in the two contemporary groups. In comparison, historical wild-origin male kākākāpō had larger ceres than both contemporary groups. As bird bills can show rapid morphological adjustment to diet over generational time scales, we evaluate whether bill size differences measured could be due to differences in the nutritional environments experienced by the birds either across their life-times or over recent evolutionary time. We also discuss whether regional variation in sexual selection might account for the provenance related variation in cere size.

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INTRODUCTION

Natural history museums in Australia and New Zealand hold more than half a million bird specimens, the majority of which are study-skins (Gill 2006). For many endangered species, more individuals exist as study-skins than living birds. These skins are therefore a valuable resource for studying aspects of the endangered species biology, for example plumage or morphology, that may be otherwise challenging to conduct research on due

to species rarity (Lane 1996; Gill 2006), or requisite access restrictions on remnant populations. Data obtained from museum specimens collected from dispersed times and places can also be incorporated into comparative analyses with contemporary data, allowing for the dynamics of endangered species biogeography, ecology and evolution to be described and understood (Smith *et al.* 1995; Lane 1996; Stockwell *et al.* 2003; Hendry *et al.* 2007; Rolshausen *et al.* 2009). Despite the potential benefits of working with skins, owing to some common challenges such as specimen provenance accuracy (Gray & Renner 2016), unspecified specimen sex (Lee & Griffiths

2003) and the meaningfulness of comparing data from long-dead museum specimens to those from living or fresh specimens (Winker 1993), study-skins are typically under-utilised by ornithologists (Smith *et al.* 1995; Russell *et al.* 2013).

Attempting to overcome these challenges is worthwhile when studying skins might yield biological insights relevant to endangered species management, or when the rare species has exceptional ecological and evolutionary novelty. The kākāpō (*Strigops habroptilus*) is a good candidate species for which careful examination of museum study-skins could generate interesting results. Kākāpō are unique among the Psittaciformes, being very large, flightless and nocturnal, and the only known lek breeding parrots (Henry 1903; Merton *et al.* 1984). Concordant with their lek-based mating-system, kākāpō do not form monogamous pairs as most parrots do, and males and females have very distinct life-histories (Merton *et al.* 1984; Livezey 1992; Eason *et al.* 2006), the morphological and ecological correlates of which have not been extensively researched. Additional to their highly derived behaviour, and further evidence of their evolutionary novelty, kākāpō are one of only three extant species of Strigopoidea, the most basal superfamily of Psittaciformes (Chambers & Worthey 2013). Kākāpō are endemic to New Zealand and classified as critically endangered by the IUCN (IUCN 2016) and Nationally Critical under the New Zealand Threat Classification System (Robertson *et al.* 2013). There are only 154 known birds alive, all of which are maintained under intensive conservation management (Whitehead *et al.* 2012). Hundreds of kākāpō study-skins exist in museums worldwide however, and beginning to study these could contribute to our understanding of this highly unique parrot's basic biology.

Kākāpō became endangered due to predation by introduced mammals introduced to New Zealand (Henry 1903; Best & Powlesland 1985; Murphy & Dowding 1994; Clout & Craig 1995; Clout & Merton 1998). To save kākāpō from extinction, in the late 20th Century the Kākāpō Recovery Programme Programme (KRP) removed all kākāpō from their remaining wild habitats and established a breeding program on predator-free off-shore islands, with the largest population established on Whenua Hou (Codfish Island) in a semi-captive situation (Whitehead *et al.* 2012). Ninety-eight percent of the breeding population's founders were birds removed from the last known natural wild population, discovered in 1977 on Stewart Island (Powlesland *et al.* 1992; Powlesland *et al.* 1995). Today, the remaining founders and their descendants are all intensively managed by the KRP who collect extensive data from each bird, including standard measures of morphology

and reproductive state. Comparing the KRP data against those from museum study-skins from different geographical and temporal populations can therefore facilitate hypothesis-driven research on kākāpō evolutionary ecology.

Characters associated with the bill present as amenable for study when choosing what to compare between living kākāpō and museum specimen birds. Parrots are adapted to varied food, including tough vegetation, hard nuts and seeds. To facilitate this their rhamphotheca is comprised of hardened, dense keratin (Stettenheim 2000) that fits snugly over the underlying maxilla bone (Summers 1976). The post-mortem shrinkage experienced by museum specimens in bird species with softer "fleshier" bills (Summers 1976; Winker 1993) should therefore be reduced in parrots. Bill morphological traits are also highly labile in response to habitat-dictated dietary changes, and display strong directional selection in birds (Herrera 1977; Caroll & Dingle 1996; Grant & Grant 2002; Herrel *et al.* 2010). Rapid inter-generational morphological adjustments in response to local food environment change is particularly pronounced for bird species that have life histories characterised by low dispersal and therefore low inter-population gene-flow (Baker *et al.* 1990; Bardwell *et al.* 2001; Hendry *et al.* 2007), as in the flightless kākāpō. Rapid bill morphological change is also observed in species under quasi-natural selection settings, for example in response to dietary shifts under domestication (Champagnon *et al.* 2010) and captive rearing (Clabaut *et al.* 2009). This phenomenon, whereby trait divergence occurs over relatively short, ecological timeframes is called contemporary or rapid evolution (Hendry *et al.* 2000; Hendry 2001; Stockwell *et al.* 2003; Rolshausen *et al.* 2009). For bird bills, this process is facilitated by the genes and genetic pathways which underpin bill shape being highly flexible in their expression, and by multiple distinct pathways being able to affect morphological change during bill development (Mallarino *et al.* 2012).

Given the responsiveness of bill morphology to different physical and temporal food environments experienced by individuals within bird species, kākāpō museum study-skins and KRP data were used to test whether there were differences in the bill traits among males and females from three environmentally-distinct groups: 1) historical wild-origin birds likely to have been sourced from either of New Zealand's main islands (hereafter the "mainland"); 2) the modern wild-origin KRP founder population, 98% of which were sourced from Stewart Island where kākāpō may have persisted naturally for 10,000 years (Cullen 1967; Bull & Whitaker 1975; Powlesland *et al.* 1995); and 3) these founder's descendants – the modern non-wild kākāpō raised by KRP under semi-

captivity, predominantly on Whenua Hou. Habitat resources on Whenua Hou have not always allowed for kākāpō hens to raise their chicks without nutritional intervention by KRP (Whitehead *et al.* 2012). These interventions have included the supplementary feeding of “muesli” (Powlesland & Lloyd 1994; Clout & Merton 1998; Elliot *et al.* 2001) and proprietary pellets to kākāpō mothers who then pass these non-wild foods to their chicks, and the removal of chicks from nests for hand-rearing with proprietary diets (Clout & Merton 1998; Elliot *et al.* 2001; Eason & Moorhouse 2006; Whitehead *et al.* 2012; Waite *et al.* 2014). Individuals from these groups have therefore experienced different food environments either during their lifetimes, and in the case of the two wild-origin groups also in their recent evolutionary past, that may have led to provenance-specific variation in bill-morphology.

MATERIALS AND METHODS

Museum specimens

The Australian Museum kākāpō study-skins included in this study are listed in Table 1, along with the collection location and dates. The collection locations of the Macleay Museum specimens (NHB birds listed in Table 2) are unknown, however the majority of the specimens were collected before the 1890's.

Bird measurements

Bird measurements taken were: 1) the length of the exposed culmen taken from the inferior tip of the culmen to the superior edge of the cere along the sagittal plane; 2) culmen length, measured from the inferior tip of the culmen to the inferior edge of the cere along the sagittal plane; 3) bill gape; 4) tail length, measured from the tip of the longest tail feather to the point where the feather shaft met the body; and 5) the length of the claw on the longest toe. Cere size or “height” was calculated as exposed culmen minus culmen length.

All measurements from the modern non-wild and wild-origin birds were taken from the KRP data-set, of which the wild-origin group comprised 25 ex-Stewart Island birds and four Fiordland males. The data-set included multiple measures for some birds, taken across the individual's lifetime. For adult birds that had multiple sets of measurements taken, the average of these measures was used so that each bird was represented in analyses only once. To discount the influence of maturational stage on results, measures were taken only from adult KRP birds. Whether a bird had reached adult stage was judged as when the bill measurements stopped increasing and when the bird was more than 3 years old. The measures were collected by the KRP team using calipers for bill and claw

Table 1. Collection locations and collectors of Australian Museum kākāpō study skins used in this study (courtesy of the Australian Museum).

Specimen number	Collection location and date	Collector
0.30429	Nelson, South Island, 1912	Unknown
0.2299	Unknown, May 1888	W. Newman
A.901	Unknown, Dec 1877	Wheeler
0.11601	Unknown	Unknown
0.6160	Unknown	Unknown
PA.2963	Unknown	Unknown
0.2298	Unknown, May 1888	W. Newman
0.2297		
0.37317	Jacksons Bay, Westland, 1922	W. J. Plowden-Wardlaw
A.900	Unknown, Dec 1877	Wheeler
0.4048	Unknown, 13 March 1891	Canterbury Museum
A.12554	Unknown, March 1882	Unknown
0.30428	Nelson, South Island, 1912	Unknown

measurements and measuring tape for tail length.

L.J.G. collected all measures from museum specimens using tape and digital calipers. All measures were made from adult museum specimen birds, the status of which was determined through assessing specimen plumage. Juvenile kākāpō are distinguishable from adults within their first 16-18 months of life by their duller more olive-green and strongly barred plumage, their smaller more pointed bills, their paler grey faces (Powlesland *et al.* 2006) and their more barred and pointed wing primaries (Robertson *et al.* 2000). Any museum specimen that fitted this description was not measured.

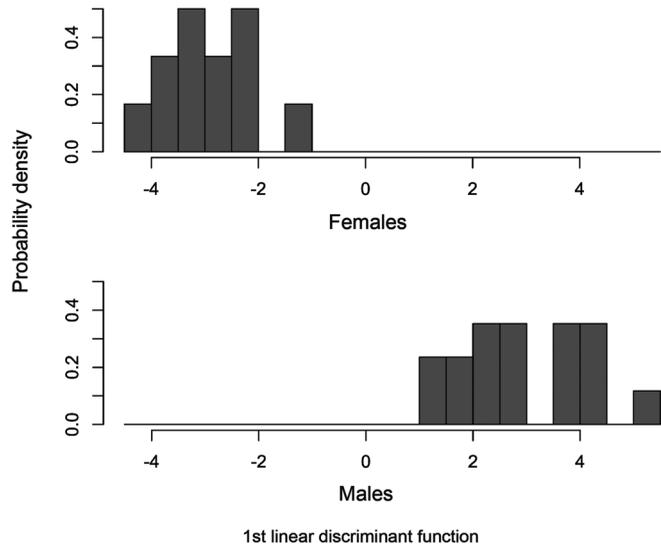
Establishing museum specimen sex

The sex of museum specimens was established by the following two methods. First, wing primary-feather patterning was analysed. Adult males have slightly broader and more rounded distal tips of their wing-primary feathers than females. Male primaries also bear faint “water-mark” patterns around the distal tip of the feathers. This patterning features on both sides of the feather mid-rib. Adult females lack these water-mark patterns on the distal tips of the wing primaries and typically bear only bar patterns on the outer edge of the feather tip mid-rib (see Robertson *et al.* 2000).

Table 2. Results from the “predicting” stage of the discriminate function analysis (DFA) and wing-primary feather pattern analysis showing final sex classification of each historical wild-origin museum specimen kākāpō.

Bird ID	DFA posterior of sex probabilities classification		DFA classification	Wing marking
	Female	Male		
0.30429	1.000000e+00	5.832189e-22	female	female
0.2299	1.000000e+00	4.180772e-16	female	female
A.901	1.000000e+00	1.148253e-28	female	female
0.11601	1.000000e+00	6.952614e-17	female	female
0.6160	1.000000e+00	3.330259e-18	female	unclear
PA.2963	NA	NA	-	male
0.2298	9.398175e-01	6.018247e-02	female	unclear
0.37317	1.000000e+00	7.776901e-15	female	female
0.900	1.000000e+00	1.667435e-19	female	unclear
0.2296	1.000000e+00	1.109244e-29	female	female
A.12555	1.150206e-05	9.999885e-01	male	male
0.37315	1.000000e+00	1.536894e-15	female	unclear
0.2297	1.000000e+00	1.956236e-14	female	female
0.4048	3.693999e-05	9.999631e-01	male	male
A.12554	1.164232e-03	9.988358e-01	male	male
0.30428	5.702767e-05	9.999430e-01	male	male
NHB-1751	1.015584e-05	9.999898e-01	male	male
NHB-1757	9.372510e-01	6.274901e-02	female	unclear
NHB-1760	1.000000e+00	8.795638e-16	female	female
NHB-1761	8.979421e-02	9.102058e-01	male	male
NHB-1758	9.790290e-01	2.097102e-02	female	female
NHB-1763	5.579903e-05	9.999442e-01	male	male
NHB-1762	9.956582e-01	4.341809e-03	female	female
NHB-1755	6.944916e-07	9.999993e-01	male	male
NHB-1750	1.000000e+00	8.272685e-12	female	unclear
NHB-1752	9.999569e-01	4.314744e-05	female	unclear
NHB-1748	9.987503e-01	1.249703e-03	female	unclear
NHB-1759	1.000000e+00	1.496819e-19	female	female
NHB-1753	6.336229e-01	3.663771e-01	female	female
NHB-1746	1.000000e+00	2.946311e-30	female	female
NHB-1747	4.326805e-02	9.567320e-01	male	unclear
NHB-1745	5.554147e-04	9.994446e-01	male	male
NHB-1756	1.000000e+00	4.713344e-08	female	female
NHB-1754	NA	NA	-	male

Fig. 1. Probability density frequency histograms from the “training” stage of the discriminant function analysis (DFA) showing how the first linear discriminant function values are distributed for modern, wild-origin female (upper panel) and male kākāpō (lower panel) of known sex.



The second method followed the approach of Arnould *et al.* (2004), whereby the KRP data were used to conduct a discriminant function analysis (DFA), trained with morphological data from wild kākāpō of known-sex, to predict the heretofore unknown sex of the wild-origin museum specimen birds. The MASS package (ver. 7.3-34) in R (ver. 3.0.2) was used to conduct a two stage DFA, trained with measures from modern wild-origin adult birds of known sex, to classify the sex of the museum birds. The measures of five traits (exposed culmen, culmen only, gape, tail length, longest-toe claw length) were used in the first stage “training” DFA in order to accommodate any differences in the level of within trait variation between the KRP data and that collected from the museum specimens (for example, due to subtle differences in measurement technique or specimen wear). The resulting DFA model was then used in a subsequent “predicting” stage of the DFA to classify the sex of the museum specimen birds on the basis of the same five traits. For cases where kākāpō sex could not be determined via wing-feather marking, the DFA prediction was accepted.

Comparing bill traits of wild-origin and non-wild birds

Multivariate analysis of variance (MANOVA) and Holm probability corrected *post hoc* multiple comparisons in R were used to test for significant differences in cere height, culmen length and bill

gape between male and female historical wild-origin kākāpō ($n = 20$ female and 11 male), modern wild-origin kākāpō ($n = 17$ female and 25 male), and non-wild adult birds hatched under KRP ($n = 36$ female and 30 male).

RESULTS

Classification of museum specimen sex

The training DFA fitted to the modern wild-origin birds was 96.6% accurate in classifying kākāpō sex. All traits showed strong sexual size-dimorphism, with the first linear discriminate function values showing no overlap across the sexes (Fig. 1). The predicting DFA classified 22 of the museum specimen birds as female and 10 as male (Table 2). Predictions of historical wild-origin kākāpō sex by the DFA were robust, in no cases did DFA classifications contradict sex designation based on wing-feather markings (Table 2). Only one bird (NHB-1753) classified as a female showed a posterior probability of an accurate classification of < 0.91 (Table 2). However, the DFA prediction of female was accepted as this posterior probability was 0.66 (therefore $> 50\%$ accurate), its first linear discriminate value was negative (-0.66) and its wing-markers indicated it was a female (Table 2). Due to missing claw and tail length data for specimens PA.2963 and NHB-1754 (the specimens were physically damaged), the DFA was unable to predict the sex of these specimens and they were excluded from subsequent analyses.

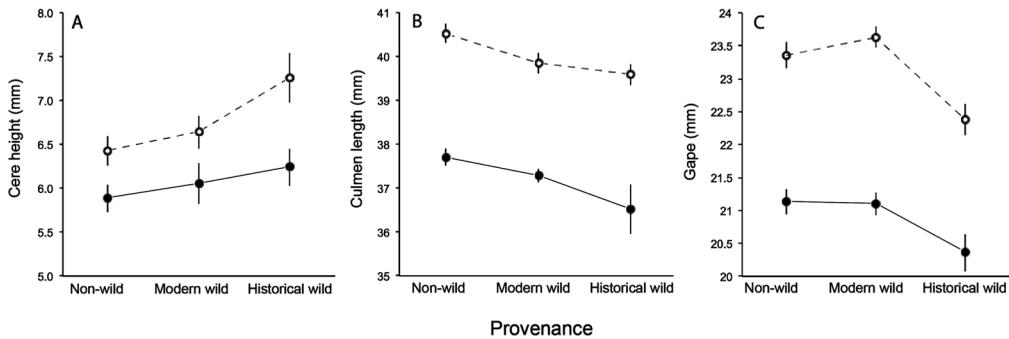


Fig. 2. Mean (\pm s.e.m) plots for kākāpō bill traits between modern non-wild, modern wild-origin and historical wild-origin females (solid line) and males (dashed line). Plots show differences in a) cere height, b) culmen length and c) gape width.

Comparison of modern non-wild kākāpō bills to those of modern and historical wild-origin birds

The multivariate component of MANOVA showed that all bill traits differed significantly with kākāpō provenance (provenance, $F_{(2, 133)} = 9.77$, $P < 0.001$). The bill traits of female and male kākāpō were also significantly different (sex, $F_{(1, 133)} = 91.72$, $P < 0.001$), with males having larger traits overall (Fig. 2). However there was no significant provenance by sex interaction of bill traits (provenance:sex, $F_{(2, 133)} = 0.69$, $P = 0.66$).

While there was a pattern for female and male kākāpō ceres to increase in size across the non-wild, to modern wild to historical wild groups (Fig 2a), the univariate component of MANOVA and *post hoc* multiple comparisons showed cere height only differed significantly between historical wild-origin males (mean = 7.25 mm) and modern non-wild males (mean = 6.42 mm) (provenance, $F_{(2, 133)} = 3.02$, $P = 0.05$, cere height non-wild male vs. historical wild Holm-corrected $P = 0.04$, Fig 2a). Cere height did not significantly differ between any other male or female kākāpō groups (Holm-corrected $P > 0.05$ for all comparisons).

Culmen length also differed significantly with kākāpō provenance (provenance, $F_{(2, 133)} = 17.17$, $P < 0.001$). Historical wild birds had the shortest bills overall, followed by the modern wild-origin then the non-wild birds which had the longest bills (Fig 2b). The opposite pattern to that shown by cere size (Fig. 2a vs. 2b). For females, *post hoc* multiple comparisons showed that culmen length differed significantly between modern non-wild and historical wild-origin birds (Holm corrected $P = 0.002$, Fig. 2b), and between modern wild- and historical wild-origin females (Holm corrected $P = 0.04$, Fig. 2b). There was no significant difference in

culmen length between the modern wild and non-wild females (Holm corrected $P > 0.05$). *Post hoc* tests showed that for male kākāpō, as in cere size, only the non-wild and historical wild-origin males differed significantly in their culmen lengths (Holm corrected $P = 0.05$, Fig. 2b). There were no significant differences in culmen length between the modern wild and historical wild-origin males or between the non-wild and the modern wild males (Holm corrected $P > 0.05$ for all comparisons).

As for culmen length, kākāpō gape width differed significantly with provenance (provenance, $F_{(2, 133)} = 20.75$, $P < 0.001$). While male kākāpō of all provenances had substantially wider gapes than female kākāpō (Fig. 2c), across the provenance groups, females and males responded similarly. For both females and males, gape width was significantly larger in non-wild birds than historical wild-origin birds (females, Holm corrected $P = 0.04$; males, Holm corrected $P = 0.01$, Fig. 2c). Modern wild-origin females and males also had significantly wider gapes than historical wild-origin kākāpō (females, Holm corrected $P = 0.04$; males, Holm corrected $P = 0.004$, Fig. 2c). There was no significant difference in gape width between the non-wild and modern wild-origin kākāpō (females, Holm corrected $P = 0.62$; males, Holm corrected $P = 0.43$, Fig. 2c).

DISCUSSION

The DFA, which classified the museum kākāpō sex with 96.6% accuracy, together with MANOVA, showed bill gape, culmen length and cere height differed significantly with provenance in female and male kākāpō. The principal differences were between the historical wild-origin birds (the

museum specimens) and the two contemporary groups – the non-wild kākāpō raised under KRP and their predominately ex-Stewart Island modern wild progenitors. These later two groups were typically statistically equivalent to one another. This pattern of similarity between the ex-Stewart Island birds and their descendants may indicate that one or two generations of exposure to KRP husbandry protocols have not substantially influenced bill trait expression. Overall, similarity between the two contemporary groups is perhaps unsurprising as most birds represented are close relatives, while their distinction from the historical wild-origin kākāpō may indicate the modern *vs.* historical birds possess unique, habitat-specific bill adaptations.

There are three potential explanations for why the modern birds' culmens were more similar to one another in their length and gape than the museum study skins. First, while the precise provenance of many of the historical kākāpō is unknown (Gray & Renner 2016), they were likely sourced from mainland New Zealand rather than Stewart Island. A viable population of kākāpō was only detected on Stewart Island in 1977 (Powlesland *et al.* 1995), though they are thought to have persisted there as a natural population potentially from the early Holocene (Cullen 1967; Bull & Whitaker 1975; Peat 1992; Powlesland *et al.* 1992; Powlesland *et al.* 1995). The ex-Stewart Island birds and their direct descendants having larger bills than the historical mainland-origin kākāpō could be because these groups are genetically distinct, and spent their recent evolutionary past adapting to unique ecological habitats.

There is a marked habitat difference between Stewart Island and mainland New Zealand that could be related to the bill length and gape differences measured here. There are no beech (*Nothofagus* spp.) trees in the forests of Stewart Island, and beech are not thought to have occurred there at all across the last 8,000 years (Hall & McGlone 2001). In contrast, beech species, which produce masses of small, nutritious fruits during their 2 to 6 yearly masting (Jensen 1982; King 1983; Ledgard & Cath 1983; Wardle 1984; Murphy 1992; Fitzgerald *et al.* 1996; Beggs 1999) are widespread across the known and likely past kākāpō habitats of the North and South islands (Wardle 1964; Atkinson & Merton 2006; Butler 2006). While kākāpō have not been observed feeding on beech flowers, fruit or seeds, they are known to browse beech leaves (Butler 2006) and *Nothofagus* species were the dominant canopy trees in the parrot's remnant Fiordland habitats (Atkinson & Merton 2006; Butler 2006). Beech masting is also thought to have triggered nesting in kākāpō maintained on Little Barrier Island in the 1990's (Harper *et al.* 2006), as it does in their close relative the kaka

Nestor meridionalis (Wilson *et al.* 1998). It is therefore possible that on mainland New Zealand, kākāpō, a previously widespread and common (Williams 1956) generalist herbivore (Powlesland *et al.* 1992; Raubenheimer & Simpson 2006), routinely fed on beech fruit and seed during masting events to support breeding. On beech-free Stewart Island, principal food plants of kākāpō known to trigger and support breeding during synchronised masting are yellow pine (*Halocarpus biformus*) and rimu (*Dacrydium cupressinum*) (Powlesland *et al.* 1992). In contrast to *Nothofagus* species, which have 2-5 mm wide and up to 6 mm long, distinctly winged dry fruits (Smissen *et al.* 2015), these Podocarpaceae trees' obovate shaped "fruits" tend to be larger (up to 8 mm wide), fleshier and softer with a hard seed attached to the top (Franklin 1968; Norton & Kelly 1988; Burrows 1994; Williams & Karl 1996). Bill morphology in birds can adapt quickly and strongly in response to changes in food item morphology, with between and within species differences in both bill length (Sulloway 1982; Weiner 1994; Smith *et al.* 1995; Grant & Grant 2002) and gape width (Rolshausen *et al.* 2009) dictating which individuals can and cannot utilise particular food sources (Sulloway 1982; Weiner 1994; Rolshausen *et al.* 2009). If kākāpō bill size is influenced by diet, mainland kākāpō incorporating large numbers of the relatively smaller, harder and uniquely shaped beech fruits in their breeding diet *vs.* Stewart Island kākāpō feeding predominately on larger softer Podocarp "fruits" could have led to the evolution of shorter, narrower bills *vs.* longer, wider bills in these respective habitats.

Considering well known examples of rapid evolution within other vertebrate species, the length of time kākāpō have persisted on Stewart Island should have allowed sufficient evolutionary time for adaptation to local conditions. For example, due to a major decline in deep-tubed, nectar rich flowers, within approximately 50 generations i'iwi honey creepers (*Vestiaria coccinea*) on Hawaii evolved shorter bills than their forebears following a necessary shift to feeding on nectar from shallow, cup-shaped flowers (Smith *et al.* 1995). *Anolis* lizards evolved shorter limbs than their ancestors following 10 to 14 generations of exposure to novel vegetation following their experimental introduction to a series of small islands near the Bahamas (Losos *et al.* 1997), and 13 generations of experimentally relaxed predation pressure led to Trinidadian *Poecilia* guppies evolving to reach sexual maturity later and at a larger size than their progenitors (Reznick *et al.* 1997). If generation time is estimated as the age differences between offspring and parents, a conservative kākāpō generation could be 15 years. Kākāpō females first breed at approximately 10 years old (Eason *et al.*

2006) and thereafter approximately every five years (Eason *et al.* 2006; Whitehead *et al.* 2012). Following this estimate, if kākāpō have been on Stewart Island for 10,000 years, they could have spent over 600 generations adapting to Stewart Island conditions. Recent molecular work comparing DNA microsatellites and mtDNA control region haplotypes between historical and contemporary kākāpō supports an isolated, historical occurrence of kākāpō on Stewart Island (Bergner *et al.* 2016). While proposals exist that the contemporary population of kākāpō from Stewart Island are descendent from six mainland birds “put to shore” in poor condition at Port Pegasus in the late 1880’s (Russ 1978), or liberated on the Island by Māori, molecular evidence suggests otherwise (Bergner *et al.* 2016). Comparisons between 48 contemporary ex-Stewart Island KRP founder kākāpō and 52 mainland kākāpō sourced across the South Island from 1884 to 1985 showed contemporary ex-Stewart Island individuals share no common mtDNA haplotypes with South Island birds, and analysis of population structure among the samples found no microsatellite overlap between the two groups (Bergner *et al.* 2016).

Alternate explanations for the bill trait size differences between historical wild-origin and modern kākāpō could include Allen’s rule, bill shrinkage in the museum specimens or genetic drift occurring between isolated populations. Allen’s rule states that as the mean daily temperature increases over time, endothermic animal’s appendages become larger in proportion to their body size to facilitate excess heat dissipation (Allen 1877; Symonds & Tattersall 2010). Studies on crimson rosella (*Platycercus elegans*) and Mulga parrot (*Psephotus varius*) collected from 1871 to 2008 have shown that for these species, bill surface area has increased by 4-10% concurrent with the ~1°C increase in Earth’s land surface temperature (Campbell-Tennant *et al.* 2015). Therefore, it is possible that the larger bill size of modern *vs.* historical kākāpō could be similarly attributed to temperature increase. Evaluating whether Allen’s rule is applicable to kākāpō bills would require a longitudinal study that measures bill-size of historical and contemporary kākāpō relative to a body-part which reliably scales with body size in birds, for example, wing-length (Campbell-Tennant *et al.* 2015) and controls for potential confounding due to museum specimen shrinkage. Conducting this analysis would simultaneously determine whether the museum specimen kākāpō had smaller bills than the modern birds due simply to being smaller birds.

Alternatively, rhamphotheca shrinkage undergone by the 140 year old museum specimens may account for the historical wild-origin kākāpō

having smaller bills (Summers 1976; Harris 1980; Norman & Brown 1987; Wilson & McCracken 2008). Studies on teal (Wilson & McCracken 2008), petrels (Norman & Brown 1987), waders (Engelmoer *et al.* 1983) warblers, flycatchers (Winker 1993) and puffins (Harris 1980) have shown that museum specimens can loose up to 3 mm, usually within the first two months of preservation, in places where the rhamphotheca is unsupported by the maxilla bone (Harris 1980). However, due to high levels of rhamphotheca morphological diversity between species, shrinkage patterns are taxon specific (Wilson & McCracken 2008). No published studies have evaluated the extent to which museum specimen parrot bills shrink, though some KRP birds included in the present study that have since passed away and are preserved as specimens could be evaluated. This will be an important next step in determining whether the bill trait size differences measured between living and museum kākāpō in the present study are due to interesting ecological and evolutionary processes or are an artefact of shrinkage.

Intriguingly, unlike culmen length and gape, the historical male wild-origin kākāpō had significantly larger cere than the two modern, related kākāpō groups, which again were statistically equivalent. There is very little published research on the functional significance of cere morphology, including for kākāpō which have very large, prominent ceres. Most work focuses on cere colour change in relation to sexual maturity or attractiveness in kaka, kea, budgerigars and falcon (Cinat-Thompson 1926; Moorhouse & Greene 1995; Mougeot & Arroyo 2006; Schmidt 2007; Abbassi & Burly 2012; Lahaye *et al.* 2014). Possibly, as for the other aspects of bill morphology investigated here, cere size could also be subject to localised selection, in this case sexual selection. Cere variation, at least in male kākāpō, may be condition dependent (Darwin 1871; Andersson 1982) and correlate with mate quality, mating capacity and mate assessment. This occurs in non-lekking budgerigars and falcons for which males with deeper blue ceres (Abbassi & Burly 2012) and more UV reflective ceres are considered more attractive respectively (Mougeot & Arroyo 2006). If mate preferences or environmental factors which dictate condition vary regionally, sexual selection could have contributed to size differences expressed between the historical wild-origin birds and the ex-Stewart Island kākāpō and their KRP raised descendants. Given their lek-based mating system (Merton *et al.* 1984), if sexual selection operates on the kākāpō cere it would do so more intensely in kākāpō than in these non-lekking species (Payne 1984; Hendry *et al.* 2007). Indeed, cere morphology may be correlated with, or contribute to, male vocalisation or “booming”

capacity. Booming is understood to represent male quality and therefore be subject to sexual-selection in kākākāpō (Merton *et al.* 1984). In female budgerigars, inducing cere colour change experimentally through testosterone administration from brown to blue simultaneously induces females to produce louder and more frequent male-type “warbling” vocalisations (Nespor *et al.* 1996; Lahaye *et al.* 2012), suggesting differences in calling behaviour and cere morphology is correlated in some parrots. A positive relationship between cere morphology and booming capacity would provide an explanation for how sexual selection might operate to influence the “appearance” of a morphological trait in the nocturnal kākākāpō. This relationship could be investigated by comparing the cere morphology of living male kākākāpō with differential booming output and mating success. Alternatively, although they appeared normal, the museum specimen kākākāpō ceres may also have been morphologically altered by the specimen preparation process or through specimen ageing. For example, the wild-origin birds’ ceres may have stretched along their sagittal plane as the body skin superior to the cere dried over time, leading to an artificial increase in height.

While the pattern was not supported statistically, contemporary kākākāpō maintained since hatch under KRP artificial diet protocols, mostly on Whenua Hou, had marginally longer and wider culmens than their ex-Stewart Island forebears. These results suggest tentatively that kākākāpō may be adapting to the feeding protocols of KRP or the environment of Whenua Hou. While the difference was subtle, as might be expected after only one or two generations of exposure to a food environment change (Champagnon 2010), the non-wild KRP birds may have variously responded to being reared on proprietorial diets as chicks (Eason & Moorhouse 2006; Whitehead *et al.* 2012), their mothers receiving supplementary food (Powlesland & Lloyd 1994; Raubenheimer & Simpson 2006; Houston *et al.* 2007), and passing it onto them as chicks, or to natural habitat differences between Stewart Island and Whenua Hou. It will be interesting to continue to monitor this trend over time as the KRP kākākāpō population continues to grow.

This study demonstrates museum specimens can provide a foundation for generating new knowledge and research questions on endangered birds. By comparing historical museum specimen kākākāpō from mainland New Zealand to contemporary ex-Stewart Island kākākāpō and their descendants, we found that specimens of historical birds had shorter, narrower culmens and larger ceres. Birds’ bills can be highly responsive to changes in habitat food sources, and in their recent evolutionary past the historical mainland kākākāpō

and the contemporary birds were likely exposed to the respective presence/absence of *Nothophagus* spp. on the mainland *vs.* Stewart Island. This synthesis supports the hypothesis that kākākāpō bill morphology is responsive to food environment differences and supports an existing idea of Harper *et al.* (2006) that kākākāpō can utilise beech masts to support breeding. These findings may have implications for kākākāpō transitioning from KRP “semi-captivity” to fully wild diets elsewhere in New Zealand within their lifetimes. If the differences measured here are real and mediated by food environment (rather than shrinkage or due to Allen’s rule), the potential exists for kākākāpō to experience mis-match between the food environment experienced in their recent evolutionary past and that experienced when released into new habitats (Stockwell *et al.* 2003; Raubenheimer *et al.* 2012).

At this stage, these conclusions are however speculative and require verification. Importantly, the role of museum specimen shrinkage in determining the differences in bill and cere size measured here needs evaluation as does whether kākākāpō are responsive to and utilise beech masting to support breeding. A possible first step toward resolving whether kākākāpō bill traits show consistent localised regional variation would be to source and sample museum specimen kākākāpō of known geographical and temporal provenance. If localised adaptations do account for the differences among kākākāpō bill traits, then morphological variation would show geographical structuring. Using historical specimens for this purpose would also ensure that the potential confounding influence of specimen shrinkage would be controlled for by all historical specimens having under gone comparable shrinkage.

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