DIGGING IN! BURROWING PENGUINS AND SURFACE PREDATORS

LAURA X.L. TAN[1]*, KASUN B. EKANAYAKE[2], WOUTER F.D. VAN DONGEN[1], PETER DANN[3],
DUNCAN R. SUTHERLAND[3] & MICHAEL A. WESTON[1]

[1]Deakin University, School of Life and Environmental Sciences, Melbourne Campus,
*221 Burwood Highway, Burwood, Victoria 3125, Australia *(L.Tan@research.deakin.edu.au)*
[2]BirdLife Australia, Suite 2-05, 60 Leicester Street, Carlton, Victoria 3053, Australia
[3]Research Department, Phillip Island Nature Parks, Cowes, Victoria 3922, Australia

Received 23 January 2022, accepted 01 June 2022

ABSTRACT

TAN, L.X.L., EKANAYAKE, K.B., VAN DONGEN, W.F.D., DANN, P., SUTHERLAND, D.R. & WESTON, M.A. 2022. Digging in! Burrowing penguins and surface predators. *Marine Ornithology* 50: 177–187.

A native Australian corvid, Little Raven *Corvus mellori*, has emerged as a dominant and problematic predator of an ecologically and economically important seabird, the Little Penguin *Eudyptula minor*. In 2013, ravens successfully preyed upon clutches/broods of the burrow-nesting penguin, especially those in shallower, more accessible burrows. Individual raven size might mediate which ravens attack penguins; smaller ravens may be able to enter burrows more easily; alternatively, larger ravens may be more capable of overcoming penguin parental defence. Here, we consider the predator-prey interactions to assess whether associations with burrow characteristics persisted and examine whether raven size mediated propensity to prey upon penguin eggs. We compared data from the 2013 and 2015 penguin breeding seasons at Phillip Island (Victoria, Australia) for differences in clutch survival and burrow characteristics. We also examined raven morphometrics to determine if any physical differences existed between known burrow-predators ("culprits") and other birds. During the 2013 breeding season, penguins suffered clutch losses of 61.1% compared with 33.9% in 2015. Burrow characteristics changed between seasons—most noticeably, burrows were deeper in 2015 and ravens no longer discriminated between burrow characteristics. Culprits were heavier and larger. While we could not eliminate inter-annual variability as a possible contributing factor, our results were consistent with rapid adaptation of prey and predator to intense emergent depredation. Penguins may now construct deeper burrows, and ravens evidently no longer select more vulnerable burrows. Larger ravens may be more capable of approaching and attacking penguin burrows.

Key words: raven, penguin, burrow, predator risk, prey response, adaptation

INTRODUCTION

Predators can drive significant adaptive responses in prey, a process that may lead to evolutionary arms races (Dawkins & Krebs 1979, Lima & Dill 1990, Conner & Corcoran 2012). Human influences—including urbanisation, resource subsidies, and species introductions—are widespread and common, and they disrupt many ecosystems and trophic structures (Schoener *et al.* 2001, Doherty *et al.* 2016, Pringle *et al.* 2019). Such disruption can alter long-standing predator-prey relationships, thereby altering evolutionary trajectories or threatening the persistence of populations (Schoener *et al.* 2001, Minnaar *et al.* 2015). This is especially detrimental to prey species for which the consequence of "losing" the arms race is loss of life (versus loss of a predator's meal), and it arguably forces prey species to adapt quickly (Dawkins & Krebs 1979). In addition to skewing existing predator-prey relationships, anthropogenic processes may also introduce new predatory pressures that prey are not equipped to deal with. While this can include the introduction of non-native invasive species, such as the red fox *Vulpes vulpes* and the cane toad *Bufo marinus* in Australia (Saunders *et al.* 2010, Shine 2010), existing native predators that are able to adapt to and benefit from anthropogenic processes may also emerge as new threats by becoming superabundant and/or exploiting disadvantaged prey (Ueta *et al.* 2003, Ueta & Hirano 2006, Ekanayake *et al.* 2015a, Doherty *et al.* 2016).

One such example of a successful, human-tolerant predator group is the family Corvidae (henceforth "corvids"), i.e., ravens, crows, rooks, and jays. In circumstances where corvids are considered problematic to prey, both corvids and prey are usually native (e.g., Ekanayake *et al.* 2015a). Their intelligence and generalist, omnivorous foraging habits contribute to corvids' ability to shift foraging strategies and exploit human-dominated environments (Brook *et al.* 2003, Ueta *et al.* 2003, Brown & Jones 2016). Indeed, corvids are renowned for their innovation, intelligence, and learning (Hunt 2000, Bird & Emery 2009, Marzluff *et al.* 2010). This likely contributes to their ability to successfully adapt to and thrive in a multitude of landscapes and subsequently target an array of prey species (Liebezeit & George 2002, Ueta & Hirano 2006, Ekanayake *et al.* 2016, McIver *et al.* 2018). In some cases, they can develop specific foraging niches, targeting and successfully exploiting certain prey groups with high specialisation and even tool use (Hunt 2000, Troscianko *et al.* 2012, Matsui *et al.* 2016). The ability to innovate and adapt so effectively contributes to their ability to successfully prey upon the eggs and chicks of species having complex antipredator adaptations, including both tree- and ground-nesting bird species (Marzluff 1988, Liebezeit & George 2002, Ekanayake *et al.* 2015c, Coates *et al.* 2020).

On Phillip Island, Victoria, Australia, one native corvid species, the Little Raven *Corvus mellori*, has emerged as a predatory threat to a seabird of conservation and economic importance, the Little Penguin *Eudyptula minor*. Little Ravens employ a relatively novel predatory behaviour on penguin clutches at this location, and this depredation appears to be targeted and intense. Specifically, Little

Ravens have been recorded preying upon up to 61.1% of monitored penguin clutches, whereby eggs or chicks are extracted from an actively defended burrow by ravens working either singly or in pairs (Ekanayake *et al.* 2015a). Despite long-term monitoring of the penguin population since 1977 (Dann 1991), raven predatory behaviour at penguin burrows on the Summerland Peninsula (where the main penguin colony on Phillip Island is located) has been observed only within the past 25 years (Nakazawa 2004, Swinburne & Jessop 2005, Ekanayake *et al.* 2015a). Clutches are extracted either straight through the burrow entrance or by digging a hole in the burrow's wall or ceiling; for details of burrows and the nature of Little Raven attacks, refer to Ekanayake *et al.* (2015a). Where attacks have involved two ravens (often suspected to be breeding pairs; KBE unpubl. data), cooperative behaviour is sometimes observed, whereby one raven "distracts" the adult penguin while the other accesses the clutch (Ekanayake *et al.* 2015a). To successfully prey upon penguins, ravens first must locate an active burrow, determine its contents (as burrow occupancy varies temporally and spatially; Sutherland & Dann 2014), then access the eggs/young by overcoming any defence mounted by the adult penguin. As adult Little Penguin body mass ranges from 550–2130 g compared to 421–650 g for Little Ravens (Marchant & Higgins 1990, Higgins *et al.* 2006), direct confrontations are likely a challenge for the ravens, although they are physically larger (48–52 cm vs. 40–45 cm length for ravens and penguins, respectively; Marchant & Higgins 1990, Higgins *et al.* 2006). Exploitation of burrow nests by corvids has also been observed at another Little Penguin colony at Port Campbell in western Victoria (G. Sutton pers. comm.), although not to the same extent as in the Ekanayake *et al.* (2015a) study. Burrow-raiding by corvids has been recorded for other burrow-nesting bird species, including Razorbills *Alca torda*, Rhinoceros Auklets *Cerorhinca monocerata*, and Burrowing Owls *Athene cunicularia* (Hudson 1982, Blight *et al.* 1999, Hayward *et al.* 2015, Henderson & Trulio 2019), and for rabbits (Mykytowycz *et al.* 1959). Instances of depredation by other corvids at seabird crevice nests has also been reported (McIver *et al.* 2018).

Intense depredation by new or existing predators may elicit altered behaviour in prey species (Eggers *et al.* 2006, Massaro *et al.* 2008, Conner & Corcoran 2012). Depredation risk in birds can mediate nest site choice, adult/chick behaviour, and construction of "safer" nests. Safer nests may be created by reducing potential cues used by predators to locate prey (Marzluff 1988, Massaro *et al.* 2008, Chen *et al.* 2011, Haff & Magrath 2011) or by increasing physical protection that limits predator access or penetrability (Hudson 1982, Regehr *et al.* 1998, Stokes & Boersma 1998). While burrows confer visual concealment and physical protection (Hudson 1982, Warren 1990, Ekanayake *et al.* 2015a), the selection of specific burrow traits may also affect depredation risk (Stokes & Boersma 1998). Certain burrow-using species may adapt behaviour or burrow design/traits based on predator risk (Griffiths & Richardson 2006, Chen *et al.* 2011).

Little Penguins are a burrow-nesting species and chicks primarily rely on the protection of a parent and/or the safety of the burrow itself to avoid predators (Warham 1958, Chiaradia & Kerry 1999, Ekanayake *et al.* 2015a). At least one parent remains in the burrow to incubate and protect the clutch until eggs hatch and chicks are two weeks old (Chiaradia & Kerry 1999). At that point, thermoregulatory and depredation risks associated with age/size may be lessened (Cerchiara 2018). Little Penguin adult pairs are more likely to shift burrows after a failed breeding attempt (Reilly & Cullen 1981, Bull 2000), which may be an adaptive response enabling adults to find or construct a burrow that is less vulnerable to failure caused by poor burrow structure or predator attacks (Young 1994, Bull 2000, Ekanayake *et al.* 2015a). Corvids tend to use visual and auditory cues to detect prey, relying less on olfactory cues (Santisteban *et al.* 2002, Ekanayake *et al.* 2015b, Husby 2019). Little Penguin parents remain in the burrow by day when corvids are active. Factors such as greater burrow depth may confer the advantage to penguins (over Little Ravens), making penguins less detectable (i.e., fewer auditory, visual, or other cues) or more resistant to predator attack (Griffiths & Richardson 2006, Leighton *et al.* 2009, Ekanayake *et al.* 2015a). Other burrow traits, such as narrow entrance sizes, may also be important in preventing predator access (Stokes & Boersma 1998, Duffy & Capece 2014, Ekanayake *et al.* 2015a).

Corvids exhibit individual variation in terms of morphology, intelligence, and behaviour (Range *et al.* 2006, Shannon *et al.* 2014, Brown & Jones 2016). In the same way that New Caledonian Crows *Corvus moneduloides* have developed behavioural and morphological features benefiting their tool use and exploitation of prey (Hunt 2000, Troscianko *et al.* 2012, Matsui *et al.* 2016), certain aspects of an individual raven's morphology or behaviour may assist successful burrow exploitation (Brown & Jones 2016, Tan *et al.* 2021). Little Raven females are smaller than males and are more likely to squeeze through smaller apertures to obtain food rewards (Shannon *et al.* 2014). Thus, body size affects a raven's ability to prey upon clutches in burrows: smaller ravens may be able to access penguin burrows more easily (either from the entrance or through raven-created openings), while larger ravens may be more capable of confronting and circumventing a defending adult penguin (*sensu* Richner 1989). A larger body size may also be associated with a raven being bolder or more dominant (Richner 1989) and, hence, more likely to approach an active burrow.

This study aimed to: 1) examine whether penguins have adapted their behaviour due to the high rate of clutch depredation observed by Ekanayake *et al.* (2015a) by selecting burrows that are less vulnerable to raven attack; and 2) determine if raven "culprits" (i.e., ravens observed preying upon penguin eggs or chicks) possessed morphological traits that facilitate burrow-raiding behaviour and distinguish them from "other" birds (i.e., ravens not observed preying on penguin eggs/chicks). We hypothesised that penguins preferentially selected or persisted more commonly in 1) protective burrows (i.e., those with deeper, narrower entrances) and 2) burrows in which detection of prey is more difficult (i.e., a smaller amount of bare ground at the burrow entrance). We also expected that 3) individual size mediates a corvid's likelihood of attacking a burrow (i.e., either smaller birds are more capable of penetrating a burrow or larger birds are more capable of overcoming the defending parent).

METHODS

Study site

Phillip Island is located on the south-central coast of the state of Victoria in Australia. Its main Little Penguin colony is located on the western end of the island's Summerland Peninsula (38.51°S, 145.13°E). Penguin colonies are located on both the southern and northern coasts of the peninsula (Sutherland & Dann 2014). Following Ekanayake *et al.* (2015a), burrow monitoring was conducted within two sections on the southern coastal side between

September 2015 and February 2016 (henceforth 2015) to compare to previous monitoring conducted between September 2013 and December 2013 (henceforth 2013). Nests were also monitored on the northern side of the peninsula in 2015, but these observations were used only to identify culprits (Tan *et al.* 2021). Otherwise, burrows were selected from the same areas in each year. Raven trapping (to colour-band birds for individual identification and to identify culprits; see **Methods**) was conducted across the entire Summerland Peninsula from 2012 to 2017. The primary trapping methods involved the use of wire cage traps (710 × 310 × 305 mm) and a modified Australian Crow Trap (Tan *et al.* 2021), with effort concentrated towards trapping corvids in penguin breeding areas and areas with high densities of ravens (see Tan *et al.* 2021 for a map detailing specific burrow and raven-trapping locations).

Burrow monitoring

A burrow was initially selected for monitoring if it contained at least one adult penguin and at least one egg (of a typical clutch of two; Reilly & Cullen 1981). Only clutches that reached two eggs during subsequent monitoring were included in final analyses (i.e., where it was certain that no successful depredation occurred before a full clutch was achieved). Nest success was attributed to burrows in which penguins successfully raised either a) both chicks to at least 2 weeks of age (at which point parents no longer guard chicks and chicks are more likely to be able to defend themselves; Chiaradia & Kerry 1999, Cerchiara 2018) or b) a single chick to at least 2 weeks of age and where the other egg was determined to be infertile or the other chick perished due to non-predatory causes such as starvation or crushing (i.e., where no depredation was apparent). Nest failure was attributed to burrows in which at least one egg/chick was preyed upon (i.e., found missing on weekly burrow checks or confirmed depredated via camera footage; see below). Nest abandonment was defined as situations in which eggs failed to hatch and/or the nest was abandoned. This was the only other detected cause of nest failure (Ekanayake *et al.* 2015a, this study); these nests were excluded from the data set. Collectively, nest success or failure is referred to as its fate. Monitored burrows were checked weekly until nest fate was determined.

Cameras were used to help determine burrow fate and to identify culprits. Cameras were deployed during the first check for every second monitored burrow within the study site. Cameras (Scoutguard 5 MP DTC-530 V) were installed 2–3 m from burrow entrances on a 90 cm stake, ~20 cm off the ground, and facing the burrow's entrance. Camera traps were set to record bursts of three images with no delay between triggers. Burrows monitored without cameras were used as a control to determine whether cameras influenced the rate of depredation (Ekanayake *et al.* 2015a). These control burrows were marked by a small 20–30 cm stake.

Burrow characteristics

Burrow characteristics were measured by two different researchers in 2013 and 2015. After removal of non-comparable sites, missing data, and abandoned nests, we measured 203 burrows in 2013 and 177 in 2015. Ekanayake *et al.* (2015a) measured eight burrow characteristics during the 2013 season that may have contributed to burrow-raiding susceptibility. These were: 1) burrow depth, 2) entrance height, 3) entrance width, 4) thickness of burrow roof at burrow entrance, 5) curvature of the burrow tunnel, 6) vegetation type above the burrow, 7) area of faecal excretion ("whitewash") at the entrance, and 8) area of bare ground at the burrow entrance. Area of bare ground and whitewash were measured because they were deemed to be characteristics that may provide visual cues to ravens, and the remaining characteristics were measured due to their potential to limit raven access to eggs and chicks (Ekanayake *et al.* 2015a). A detailed description of these characteristics and how they were measured is provided in Ekanayake *et al.* (2015a). A ninth characteristic, distance to next burrow (regardless of occupation), was also recorded in 2013 (but not published) and 2015. Proximity to other burrows may influence the likelihood of a burrow being investigated or attacked by a raven, or it may influence a burrow's susceptibility due to factors related to burrow density (e.g., Clark *et al.* 2019); thus, it was included in the present analysis.

All measurements recorded in 2013 (Ekanayake *et al.* 2015a) were replicated in the 2015 season. Confidence intervals for mean monthly air temperatures overlapped between the seasons studied (2013: 17.3–21.3 °C; 2015: 17.5–24.7 °C). Following these two seasons of data collection, we conducted a blind measure comparison of a set of burrows to enable adjustment of any measurement bias (performed by KBE and LXLT for 2013 and 2015, respectively). Regression analysis indicated that four of the eight traits (burrow depth, entrance width, area of bare ground at entrance, and distance to next burrow) were sufficiently consistent between observers to use for analysis (linear regressions, $R^2 > 0.70$), and data for the 2015 season were corrected to account for observer differences (Table S1 in Appendix, available on the website). Assessments of vegetation type were consistent between observers and were also included. We compared these five burrow traits between seasons.

Raven morphometrics

Between 2012 and 2017, 198 ravens were trapped and banded in or near the penguin colony as per Tan *et al.* (2021). Each captured raven's right tarsus was fitted with a unique metal ring provided by the Australian Bird and Bat Banding Scheme (ABBBS). Each bird was also fitted with a three-digit engraved colour band on its left tarsus for visual identification from a distance. We took morphometric measurements as used by Shannon *et al.* (2014) and as measured by Rowley (1970), as well as blood and feather samples for genetic sexing; see Tan *et al.* 2021 for details. Alongside standard measurements of body mass, wing length, tail length, tarsus length, and head plus bill length, we examined four bill measurements (Fig. 1): bill length (Bill A), nostril to tip (Bill B), width of bill at nostril (Bill C), and bill depth (Bill D). Body mass was measured to the nearest gram, and all other measurements were recorded in millimetres to two decimal places.

Culprit identification

Culprit birds were primarily identified through images captured by remote-sensor cameras placed on penguin burrows over the two breeding seasons analysed in this study. No ravens were observed preying upon adult penguins. We supplemented images from the 2013 and 2015 breeding seasons with images obtained from a separate third season (2016/17; see Tan *et al.* 2021). Briefly, all viable images were reviewed to identify Definite Culprits (DC, banded individuals who had been identified actively preying on penguin eggs or small chicks at burrows) and Possible Culprits (PC, banded individuals that were seen visiting penguin burrows but with

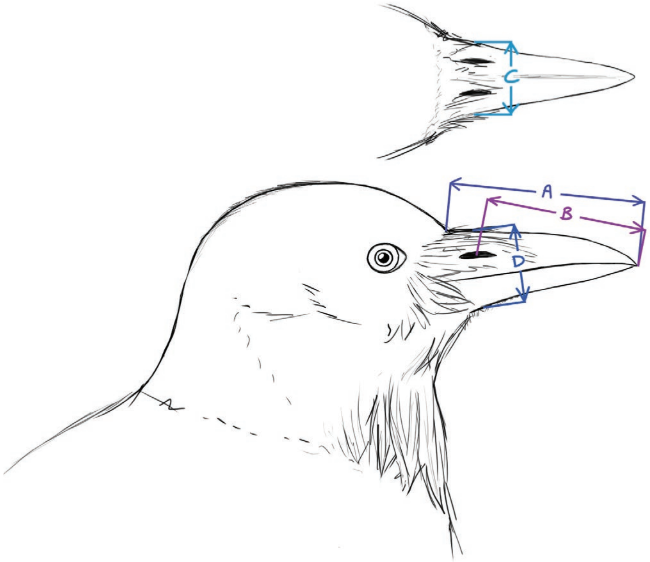

Fig. 1. The four bill measurements used in this study, redrawn and adapted from Rowley (1970): Bill A (bill length), Bill B (nostril to tip), Bill C (width of bill at nostril), and Bill D (bill depth).

no evidence of active depredation). Collectively, these birds are referred to as Definite and Possible Culprits (DPC). All remaining banded ravens, i.e., individuals that had been banded during trapping but were not seen at penguin burrows, were classified as Other Birds (OB). We included PC in the OB category for comparisons of DC and OB. We use the term "Other Birds" because we cannot be entirely certain that these birds are non-culprits.

We accept that some culprits may have been missed and mis-categorised as OB; however, in the majority of occasions, culprits tended to make repeat visits to burrows, allowing for subsequent identification (LXLT unpubl. data). Similarly, individuals not posing a direct threat to clutches at a burrow (e.g., foraging on other items in the burrow vicinity) may be mistakenly identified as PC, although presence at a burrow is the first step towards implementing trial and error methods that may lead to successful burrow attacks (Tan *et al.* 2021). Significant effort was directed at determining the identity of culprits (*ca.* 660 field-days, *ca.* 270 days of image coding, 6.40 million images reviewed), and we have a high degree of confidence in our overall assignment of individuals to groups. The majority of photos (4.16 million images) were coded by manually reviewing images; the remaining 2.24 million images were coded aided by automated photo-recognition methods (Tan *et al.* 2021).

To identify differences in morphometrics between culprits and other birds, we excluded any bird that was not identified as an adult (i.e., examining only birds that had completely white eyes; Rowley 1970). We further excluded two individuals that were captured with pre-existing deformities. Where there were multiple measurements for an individual, we included the first record where the bird was determined to be an adult.

Statistical analysis

Burrow analysis

Initial results indicated that burrow characteristics were barely to moderately correlated: Pearson's correlation coefficients (r) ranged between −0.474 and 0.343. We used multivariate analyses to examine burrow characteristics across seasons and in relation to whether they were successful. Data were normalised before generating a Euclidean resemblance matrix. To examine differences between nest fate and season (2013, 2015), we conducted a two-factor permutational multivariate analysis of variance (PERMANOVA) on burrow characteristics in PRIMER v.7 (Anderson *et al.* 2008). We performed permutational analyses of multivariate dispersions (PERMDISP) to examine differences in dispersion for fate and season. Upon finding a significant interaction between fate and season, we ran a canonical analysis of principal coordinates (CAP) on the interaction term, which allowed us to visualise the data using a constrained ordination plot (Anderson & Willis 2003).

To supplement the multivariate analysis, we conducted separate full factorial univariate two-factor general linear models (GLM) in SPSS v.26 (IBM Corp 2019) on each burrow characteristic against two fixed categorical factors, namely Fate and Season (Table 1). We present these results below for completeness, recognising that the

TABLE 1
Univariate general linear model results for burrow characteristics against nest fate (success, failed) and season (2013, 2015) for Little Penguins *Eudyptula minor*[a]

Burrow characteristic	**Fate**	**Season**	**Fate*Season**	**R^2 (Adjusted R^2)**
Burrow depth (cm)	$F_{1,376} = 278.326$, $\eta^2 = 0.425$, **$P < 0.001$**	$F_{1,376} = 637.204$, $\eta^2 = 0.629$, **$P < 0.001$**	$F_{1,376} = 116.404$, $\eta^2 = 0.236$, **$P < 0.001$**	0.784 (0.782)
Entrance width ($\log_{10}$ cm)	$F_{1,376} = 461.127$, $\eta^2 = 0.551$, **$P < 0.001$**	$F_{1,376} = 750.287$, $\eta^2 = 0.666$, **$P < 0.001$**	$F_{1,376} = 365.880$, $\eta^2 = 0.493$, **$P < 0.001$**	0.796 (0.794)
Area of bare ground (cm^2)	$F_{1,376} = 17.428$, $\eta^2 = 0.044$, **$P < 0.001$**	$F_{1,376} = 55.349$, $\eta^2 = 0.128$, **$P < 0.001$**	$F_{1,376} = 29.324$, $\eta^2 = 0.072$, **$P < 0.001$**	0.208 (0.201)
Distance to next burrow ($\log_{10}$ cm)	$F_{1,376} = 38.398$, $\eta^2 = 0.093$, **$P < 0.001$**	$F_{1,376} = 13\ 1.379$, $\eta^2 = 0.259$, **$P < 0.001$**	$F_{1,376} = 20.757$, $\eta^2 = 0.052$, **$P < 0.001$**	0.316 (0.311)
Vegetation type	$F_{1,376} = 0.342$, $\eta^2 = 0.001$, $P < 0.559$	$F_{1,376} = 4.758$, $\eta^2 = 0.012$, **$P = 0.030$**	$F_{1,376} = 2.844$, $\eta^2 = 0.008$, $P < 0.093$	0.023 (0.015)

[a] Partial *eta* squared (η^2) provides information on effect size; significant results $P < 0.05$ indicated in **bold** text

individual response variables were highly correlated. Variables were transformed, as required, to normality.

Raven morphometrics

Initial results indicated that raven morphometric characteristics were moderately to highly correlated (Pearson's *r*: 0.208–0.895). To account for this and to reduce the data to uncorrelated components, a principal components analysis (PCA) with varimax rotation was conducted. This resulted in two components, and we analysed the scores for each using linear mixed models. We set sex and culprit status as fixed effects and season as a random effect, to account for the different observers between years. Cohen's *d* was also calculated separately to describe effect size.

RESULTS

After exclusions, 158 individual ravens remained in the study (55 DPC [22 female, 33 male], 103 OB [46 female, 57 male]). We also examined 14 DC (6 female, 8 male) against 144 OB (62 female, 82 male; Table S2, due to the unbalanced comparison). The unbalanced DC against OB comparison was conducted to confirm that there was no substantial difference to the combined DPC group and to ensure the DPC was a relatively reliable representative of the DC group.

Burrow characteristics: Changes between years

Clutches at 61.1% of monitored Little Penguin burrows were preyed upon by ravens during 2013 ($n = 203$), compared with 33.9% in 2015 ($n = 177$; total $n = 380$, $\chi^2_1 = 27.993$, $P < 0.001$). Univariate GLMs revealed that four of the five analysed burrow characteristics (burrow depth, entrance width, area of bare ground, and distance to next burrow) featured significant main effects of Fate and Season, as well as significant interactions between these. The exception was vegetation type, which featured only a main effect of Season (Table 1, Fig. 2). A PERMANOVA revealed significant differences in burrow characteristics for the factors Fate (Pseudo-$F_{1,376} = 62.987$, $P = 0.001$), Season (Pseudo-$F_{1,376} = 134.540$, $P = 0.001$), and Fate*Season (Pseudo-$F_{1,376} = 38.027$, $P = 0.001$). PERMDISP also showed a significant interaction for Fate*Season ($F_{3,376} = 50.719$, $P = 0.001$). PERMANOVA pair-wise comparisons revealed a significant difference between burrows in 2013 that were "preyed upon" and "not preyed upon" ($t = 10.508$, $P = 0.001$). However, no significant difference was found for burrow fate amongst burrows in 2015 ($t = 1.627$, $P = 0.139$; Fig. 3).

Raven morphometrics

A PCA resolved raven morphometrics into two components with eigenvalues > 1 (Table S3). The first component (termed here "structural body size") explained 49.7% of variation with high reliability (Cronbach's $\alpha = 0.900$) and featured high positive loadings (i.e., > 0.75) with all bill, head plus bill, and tarsus measurements. The second component (termed here "flight surfaces") explained 26.4% of variation ($\alpha = 0.805$) and featured high positive loadings (i.e., > 0.80) with wing and tail length. Linear mixed models of these PCA scores revealed a difference in the structural body size of culprits, whereby culprits were larger when DPC were compared with OB (Table 2). While DC compared with OB did not reach significance for the same measure (possibly due to the low sample size of DC individuals), it tended towards significance (i.e., $P < 0.100$, in this case $P = 0.082$; Table S2). These analyses also showed that the means of all characteristics were larger in males (Table 2). Univariate linear mixed models found that mass, nostril to bill tip, width of bill at nostril, and tarsus were significantly larger in DPC individuals than OB individuals, and that all raven morphometric measures were significantly associated with sex, with males being larger than females for all traits (Table 2).

DISCUSSION

Ravens have emerged as a major predator of Little Penguin clutches on Phillip Island within the past 25 years (Nakazawa 2004, Swinburne & Jessop 2005, Ekanayake *et al.* 2015a). We uncovered two notable results: first, there appears to be substantive variation between years in predator-prey interactions which, although not definitive, are consistent with an underlying, ongoing evolutionary "arms race" between burrow-nesting penguins and ravens. Second, individual ravens we observed attacking penguin burrows tended to be larger than those that did not.

Based on our results, changes in the characteristics of penguin burrows over time may be due either to altered predator behaviour, prey behaviour, or both. These changes occurred in the context of intense initial predatory pressure directed at penguins using a particular burrow type. In 2013, 61.1% of clutches preyed upon were in exclusively shallow, open-entry burrows. By 2015, burrows had changed in form, loss rates had almost halved (to 33.9%), and ravens were less selective in the type of burrow they attacked. We noted that not all burrow characteristics changed between years, but those under the most direct influence of the penguin (e.g., burrow depth) appeared to be plastic between seasons. Deeper burrows provided advantages by displacing predator pressure to conspecifics with shallower burrows or other more accessible prey (*sensu* Griffiths & Richardson 2006), or by aiding nest concealment and survival through physically placing a clutch out of a predator's sight and reach (Leighton *et al.* 2009, Chen *et al.* 2011). Although we did not measure burrow occupancy rates, increased burrow depth could also be the result of intraspecific competition, represented by decreased distance to next burrow in 2015. This has been observed in the Sooty Shearwater *Ardenna grisea*, in which individuals dig deeper burrows in crowded areas (Clark *et al.* 2019). We also noted that some burrow characteristics did not change as hypothesised, most notably entrance width, which was wider in 2015 when depredation was lower.

Together, the changes over time in burrow characteristics, loss rates, and reduced selectivity of raven attacks on particular burrow types could be interpreted as an adaptive response of prey and/or predator. Penguins may construct or select more secure burrows, and ravens may expand their foraging niche to exploit these more secure burrows, thereby realising lower foraging success. Given that we have data from only two seasons, it is also possible that the differences represent inter-annual variation in either or both of predator or prey behaviour. For example, ravens may experience years in which there is an increase in the availability of high-quality non-penguin food sources, possibly lessening the need to prey upon penguin clutches (*sensu* Griffiths & Richardson 2006). We consider it unlikely, however, that an alternative raven food supply explains the decrease in penguin clutch loss seen in 2015—despite a decrease in vulnerable burrows in 2015, ravens began targeting a greater range of burrow types, indicating that they still sought penguin clutches. Another possible explanation is that penguin burrow characteristics influence nest microclimate, which could be important for breeding success and thermoregulation (e.g., Colombelli-Négrel 2019). Also, the observed difference in burrow types between seasons could have been a response to prevailing climate or other factors.

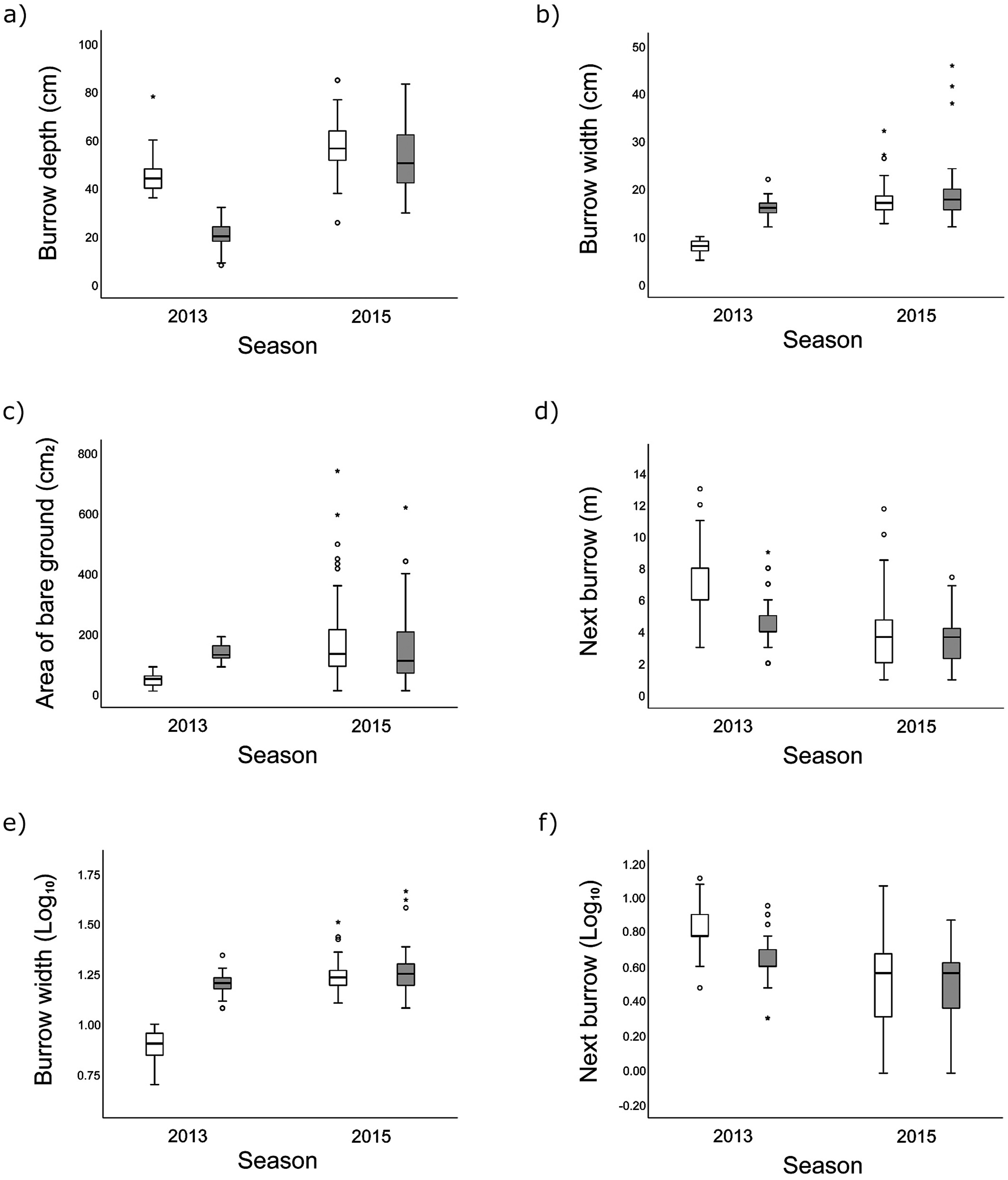

Fig. 2. Boxplots of season and fate (success, white; preyed upon, grey) of raw results for: (a) burrow depth, (b) burrow width, (c) area of bare ground at the burrow's entrance, and (d) distance to next burrow. Log_{10} transformed data are shown for (e) burrow width and (f) distance to next burrow.

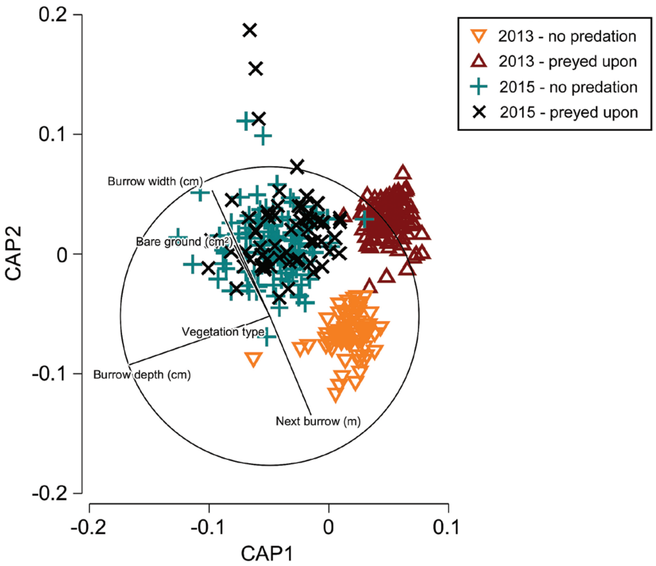

Fig. 3. Canonical Analysis of Principal Coordinates (CAP) plot presenting constrained ordination visualisation of penguin burrow characteristics over two breeding seasons, according to nest fate (failure or "preyed upon" vs. success or "no predation") and season (2013 vs. 2015). The overlaid vectors indicate the direction of change for each analysed burrow characteristic.

Penguins undergo substantive fluctuations in energetic constraints based on food availability, such that food-poor years result in poor breeding success and reduced adult survival (Dann *et al.* 2000, Chiaradia *et al.* 2010). Presumably this also affects the availability of energy that can be directed towards building or modifying burrows. Concurrently, corvids are flexible in their foraging strategies, successfully exploiting both common and specialised food sources in a variety of environments (Hunt 2000, Liebezeit & George 2002, Ueta *et al.* 2003, Ekanayake *et al.* 2015c, Coates *et al.* 2020). We were unable to unambiguously differentiate inter-annual variation from an "arms race," and we acknowledge that additional data collection is required to see if any patterns exist. Similarly, we did not track the burrow selection of marked penguins, meaning that any within-animal adaptation is inferred rather than demonstrated. Optimal foraging theory suggests that predators will optimise the energy gained relative to the energy expended in accessing prey (Pyke *et al.* 1977). It is possible that shallow burrows optimised foraging for ravens in 2013, and the abundance of penguin prey in these shallow burrows effectively protected eggs and chicks in deeper burrows from attacks that season (Griffiths & Richardson 2006, Leighton *et al.* 2009). The reduced number of vulnerable burrows in 2015 (perhaps because of previous predatory impacts or selection against those penguins) may have prompted ravens to engage in less efficient attacks on deeper and therefore less vulnerable burrows.

TABLE 2

Linear mixed model results for Little Raven *Corvus mellori* morphometrics (and standardised factor scores for principal components) with mean ± standard error (*n*) for fixed effects, namely sex (female, male) and culprit status (Definite and Possible Culprits DPC, Other Birds OB). Season is specified as a random effect.[a, b]

Characteristic	Female	Male	DPC	OB	Sex	Culprit
Structural body size	−0.540 ± 0.292 (49)	0.639 ± 0.289 (51)	0.268 ± 0.297 (34)	−0.168 ± 0.286 (66)	**$F_{1,96.1} = 63.035$, $d = -0.794$, $P < 0.001$**	**$F_{1,96.2} = 7.671$, $d = 0.277$, $P = 0.007$**
Flight surfaces	−0.733 ± 0.529 (49)	0.241 ± 0.528 (51)	−0.255 ± 0.533 (34)	−0.237 ± 0.525 (66)	**$F_{1,96.0} = 35.975$, $d = -0.600$, $P < 0.001$**	$F_{1,96.1} = 0.011$, $d = -0.010$, $P = 0.917$
Mass (g)	479.207 ± 6.682 (49)	541.877 ± 6.461 (55)	518.252 ± 7.178 (34)	502.832 ± 6.139 (70)	**$F_{1,100.2} = 99.219$ $d = -0.977$, $P < 0.001$**	**$F_{1,100.9} = 5.256$, $d = 0.225$, $P = 0.024$**
Bill A (mm)	52.202 ± 0.284 (49)	55.982 ± 0.269 (55)	54.352 ± 0.331 (34)	53.833 ± 0.231 (70)	**$F_{1,101.0} = 99.753$, $d = -0.979$, $P < 0.001$**	$F_{1,101.0} = 1.658$, $d = 0.126$, $P = 0.201$
Bill B (mm)	37.244 ± 0.242 (49)	40.180 ± 0.229 (55)	39.233 ± 0.282 (34)	38.191 ± 0.196 (70)	**$F_{1,101.0} = 82.920$, $d = -0.893$, $P < 0.001$**	**$F_{1,101.0} = 9.219$, $d = 0.298$, $P = 0.003$**
Bill C (mm)	16.365 ± 0.461 (49)	17.553 ± 0.458 (55)	17.210 ± 0.466 (34)	16.707 ± 0.456 (70)	**$F_{1,100.0} = 47.674$, $d = -0.677$, $P < 0.001$**	**$F_{1,100.1} = 7.438$, $d = 0.267$, $P = 0.008$**
Bill D (mm)	17.297 ± 0.135 (49)	18.380 ± 0.129 (55)	17.974 ± 0.147 (34)	17.702 ± 0.121 (70)	**$F_{1,100.3} = 58.310$, $d = -0.749$, $P < 0.001$**	$F_{1,101.0} = 3.228$, $d = 0.176$, $P = 0.075$
Head plus bill (mm)	95.835 ± 0.356 (49)	100.308 ± 0.337 (55)	98.405 ± 0.415 (34)	97.739 ± 0.289 (70)	**$F_{1,101.0} = 88.794$, $d = -0.924$, $P < 0.001$**	$F_{1,101.0} = 1.739$, $d = 0.129$, $P = 0.190$
Tarsus length (mm)	59.168 ± 0.385 (49)	61.907 ± 0.370 (55)	61.098 ± 0.419 (34)	59.977 ± 0.348 (70)	**$F_{1,100.2} = 48.769$, $d = -0.685$, $P < 0.001$**	**$F_{1,101.0} = 7.153$, $d = 0.262$, $P = 0.009$**
Wing length (mm)	327.827 ± 4.314 (49)	339.969 ± 4.291 (52)	334.368 ± 4.366 (34)	333.428 ± 4.259 (67)	**$F_{1,97.0} = 49.353$, $d = -0.699$, $P < 0.001$**	$F_{1,97.1} = 0.262$, $d = 0.051$, $P = 0.610$
Tail length (mm)	201.966 ± 2.898 (49)	212.537 ± 2.871 (53)	207.825 ± 2.956 (34)	206.678 ± 2.837 (68)	**$F_{1,98.1} = 51.517$, $d = -0.711$, $P < 0.001$**	$F_{1,98.3} = 0.535$, $d = 0.072$, $P = 0.466$

[a] Significant results indicated by **bold** text

[b] Effect size (Cohen's *d*) was calculated separately ("Female - Male" and "DPC - OB" for Sex and Culprit, respectively). "Structural body size" represents a principal component constituting all bill measurements, head plus bill, and tarsus. "Flight surfaces" represents a principal component with positive loadings > 0.5 against wing and tail length.

The patterns we observed indicate that culprits tend to be larger. We also found that females were smaller, that either sex could attack burrows, and that culprits were (or tended to be) heavier and larger-billed than non-culprits. Although slightly sexually dimorphic in size, the sex of Little Ravens did not appear to be a significant determinant of culprit behaviour (Tan *et al.* 2021), despite the apparent propensity of females to squeeze through narrower openings (Shannon *et al.* 2014). Optimal raven morphological traits for burrow-raiding might differ depending on the mode of attack used. A smaller body size could be more advantageous for digging attacks that involve slipping through small raven-created openings to seize an egg or chick (*sensu* Duffy & Capece 2014, Shannon *et al.* 2014). A larger raven might, however, be bolder and/or strong enough to take on an adult penguin via a main entry attack. Foraging strategies can differ between individuals based on morphological traits. For example, bill shape influences feeding method and diet specialisation in Eurasian Oystercatchers *Haematopus ostralegus* (Durell *et al.* 1993), and body size affects diving depth in Kerguelen Shags *Leucocarbo verrucosus* (Cook *et al.* 2013). Here we were unable to measure attack specialisation in Little Ravens; however, if ravens were specialising in a specific mode of burrow entry, we might expect their morphology to relate accordingly (Pyke *et al.* 1977, Durell *et al.* 1993, Cook *et al.* 2013).

Larger body size within a species may lead to variation in foraging strategy that reduces inter or intraspecific competition (Rowley 1973, Rowley & Vestjens 1973, Richner 1989). Amongst corvids, larger body sizes can relate to dominance and successful access to food (Richner 1989). Bigger individuals may also be bolder, and this may influence individual foraging strategies (Richner 1989, Rockwell *et al.* 2012, Jolles *et al.* 2013). Although corvids are able to exploit food sources in novel settings despite cautious, neophobic behaviour (Brown & Jones 2016), heightened boldness and assertiveness in larger Little Ravens may facilitate a greater likelihood of investigating new potential food sources despite any risk involved (in this case, penguin burrows guarded by an adult penguin). This might help to explain the tendency for larger birds to be more frequently identified as PC. Although non-significant, even amongst our DC-only comparison, DC tended to be larger than OB (Table S2). A raven visiting a burrow is the first step towards developing burrow-raiding behaviour, hence it follows that if larger individuals are more likely to approach a burrow, they might also be more likely to learn to attack it. It is also possible that larger, more dominant individuals exclude smaller conspecifics while foraging (Richner 1989). In the present study, it might be that resident raven pairs preyed upon penguins more frequently than non-residents and that larger ravens have been able to establish territories in these rich foraging grounds (Richner 1989, Avery *et al.* 1995).

That penguins do not appear to have selected for burrows with narrower entrances is intriguing, given that culprit ravens appear to be larger and therefore more likely to be limited by smaller entrances. It is possible that burrow width is less important than other characteristics in regard to egg or chick loss by avian predators; entrance height (but not width) was a significant predictor of egg loss for Magellanic Penguins *Spheniscus magellanicus* (Stokes & Boersma 1998). Given that ravens are able to widen existing penguin burrow entrances (Ekanayake *et al.* 2015a), comparatively deeper burrows may confer more protective benefits (Griffiths & Richardson 2006, Leighton *et al.* 2009, Chen *et al.* 2011). Alternatively, modification of existing burrows may help to explain a lack of selection towards narrower entrances, with penguins either being limited energetically (i.e., less demanding to modify an existing burrow) or by availability of suitable habitat (Wiebe *et al.* 2007). External or environmental factors may also influence burrow selection and characteristics (Colombelli-Négrel 2019), particularly in the face of climatic change (Dann & Chambers 2013).

In the context of predator risk, future work could examine burrow temperature (to assess the role of microclimate) or personality/behaviour of individual Little Penguins and how they respond to predators, to better understand how these factors may interact with burrow selection. Tracking the burrow selection of marked penguins may also assist in understanding the drivers behind those decisions and confirm any within-animal adaptation. Given that corvids are also notoriously difficult to manage, trialling appropriate corvid management methods may be a prudent course of action to help safeguard the penguin population and establish an effective management solution, should the threat of clutch loss from raven attack risk population viability. Understanding how Little Ravens target penguin clutches may assist in selecting the most effective methods for corvid management (Tan *et al.* 2021).

ACKNOWLEDGEMENTS

Research was conducted in accordance with regulations of Deakin University's Animal Welfare Committee approvals A08-2011, B19-2012, and B07-2015; Department of Environment, Land, Water and Planning permits 10005849, 10006360, and 10007531; and ABBBS authorities 1763, 2955, and 3044. The ABBBS provided all of the metal bands. Funding was provided by the Holsworth Wildlife Research Foundation, BirdLife Australia's Victoria Regional Group Research Grant, Deakin University's Centre for Integrative Ecology, and Phillip Island Nature Parks (PINP). The Beach Ecology and Conservation Hub (Venus Bay) hosted the authors for aspects of write up. Thanks to Ross Holmberg (PINP), Daniel Lees, and Morgan Pretty for assistance; field work volunteers; and the rangers and staff at PINP (especially S. Murphy, A. Dallinger, and F. Gigliotti) for their support of this project. We acknowledge the Bunurong people as the Traditional Owners of the land upon which this fieldwork was conducted. We appreciate very much the comments from reviewers who in the process helped us to improve our paper.

Availability of data and material: The data sets generated and/or analysed during the current study are available from the corresponding author upon request.

REFERENCES

ANDERSON, M.J., GORLEY, R.N. & CLARKE, K.R. 2008. *PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods*. Plymouth, UK: PRIMER-E Ltd.

ANDERSON, M.J. & WILLIS, T.J. 2003. Canonical analysis of principal coordinates: A useful method of constrained ordination for ecology. *Ecology* 84: 511–525. doi:10.1890/0012-9658(2003)084[0511:CAOPCA]2.0.CO;2

AVERY, M.L., PAVELKA, M.A., BERGMAN, D.L., DECKER, D.G., KNITTLE, C.E. & LINZ, G.M. 1995. Aversive conditioning to reduce raven predation on California Least Tern eggs. *Colonial Waterbirds* 18: 131–138. doi:10.2307/1521474

BIRD, C.D. & EMERY, N.J. 2009. Rooks use stones to raise the water level to reach a floating worm. *Current Biology* 19: 1410–1414. doi:10.1016/j.cub.2009.07.033

BLIGHT, L.K., RYDER, J.L. & BERTRAM, D.F. 1999. Predation on Rhinoceros Auklet eggs by a native population of *Peromyscus*. *The Condor* 101: 871–876. doi:10.2307/1370079

BROOK, B.W., SODHI, N.S., SOH, M.C.K. & LIM, H.C. 2003. Abundance and projected control of invasive House Crows in Singapore. *The Journal of Wildlife Management* 67: 808–817. doi:10.2307/3802688

BROWN, M.J. & JONES, D.N. 2016. Cautious crows: Neophobia in Torresian Crows (*Corvus orru*) compared with three other corvoids in suburban Australia. *Ethology* 122: 726–733. doi:10.1111/eth.12517

BULL, L.S. 2000. Factors influencing Little Penguin *Eudyptula minor* egg success on Matiu-Somes Island, New Zealand. *Emu - Austral Ornithology* 100: 199–204. doi:10.1071/MU9924

CERCHIARA, J.A. 2018. Penguins. In: SWANSON, P. & SKINNER, M.K. (Eds.) *Encyclopedia of Reproduction, 2nd Edition*. Volume 6. Sydney, Australia: Elsevier. doi:10.1016/B978-0-12-809633-8.20610-9

CHEN, J.-N., LIU, N.-F., YAN, C. & AN, B. 2011. Plasticity in nest site selection of Black Redstart (*Phoenicurus ochruros*): a response to human disturbance. *Journal of Ornithology* 152: 603–608. doi:10.1007/s10336-010-0622-9

CHIARADIA, A., FORERO, M.G., HOBSON, K.A. & CULLEN, J.M. 2010. Changes in diet and trophic position of a top predator 10 years after a mass mortality of a key prey. *ICES Journal of Marine Science* 67: 1710–1720. doi:10.1093/icesjms/fsq067

CHIARADIA, A.F. & KERRY, K.R. 1999. Daily nest attendance and breeding performance in the Little Penguin *Eudyptula minor* at Phillip Island, Australia. *Marine Ornithology* 27: 13–20.

CLARK, T.J., BONNET-LEBRUN, A.-S., CAMPIONI, L., CATRY, P. & WAKEFIELD, E. 2019. The depth of Sooty Shearwater *Ardenna grisea* burrows varies with habitat and increases with competition for space. *Ibis* 161: 192–197. doi:10.1111/ibi.12631

COATES, P.S., O'NEIL, S.T., BRUSSEE, B.E. ET AL. 2020. Broad-scale impacts of an invasive native predator on a sensitive native prey species within the shifting avian community of the North American Great Basin. *Biological Conservation* 243: 108409. doi:10.1016/j.biocon.2020.108409

COLOMBELLI-NÉGREL, D. 2019. Benefits, costs and trade-offs of nesting habitat selection in Little Penguins. *Journal of Ornithology* 160: 515–527. doi:10.1007/s10336-019-01636-z

CONNER, W.E. & CORCORAN, A.J. 2012. Sound strategies: The 65-million-year-old battle between bats and insects. *Annual Review of Entomology* 57: 21–39. doi:10.1146/annurev-ento-121510-133537

COOK, T.R., LESCROËL, A., CHEREL, Y., KATO, A. & BOST, C.-A. 2013. Can foraging ecology drive the evolution of body size in a diving endotherm? *PLoS One* 8: e56297. doi:10.1371/journal.pone.0056297

DANN, P. 1991. Distribution, population trends and factors influencing the population size of Little Penguins *Eudyptula minor* on Phillip Island, Victoria. *Emu - Austral Ornithology* 91: 263–272. doi:10.1071/MU9910263

DANN, P. & CHAMBERS, L. 2013. Ecological effects of climate change on Little Penguins *Eudyptula minor* and the potential economic impact on tourism. *Climate Research* 58: 67–79. doi:10.3354/cr01187

DANN, P., NORMAN, F.I., CULLEN, J.M., NEIRA, F.J. & CHIARADIA, A. 2000. Mortality and breeding failure of Little Penguins, *Eudyptula minor*, in Victoria, 1995–96, following a widespread mortality of Pilchard, *Sardinops sagax*. *Marine and Freshwater Research* 51: 355–362. doi:10.1071/MF99114

DAWKINS, R. & KREBS, J.R. 1979. Arms races between and within species. *Proceedings of the Royal Society B* 205: 489–511. doi:10.1098/rspb.1979.0081

DOHERTY, T.S., GLEN, A.S., NIMMO, D.G., RITCHIE, E.G. & DICKMAN, C.R. 2016. Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences* 113: 11261–11265. doi:10.1073/pnas.1602480113

DUFFY, D.C. & CAPECE, P.I. 2014. Depredation of endangered burrowing seabirds in Hawai'i: Management priorities. *Marine Ornithology* 42: 149–152.

DURELL, S.E.A.L.V.D., GOSS-CUSTARD, J.D. & CALDOW, R.W.G. 1993. Sex-related differences in diet and feeding method in the Oystercatcher *Haematopus ostralegus*. *Journal of Animal Ecology* 62: 205–215. doi:10.2307/5495

EGGERS, S., GRIESSER, M., NYSTRAND, M. & EKMAN, J. 2006. Predation risk induces changes in nest-site selection and clutch size in the Siberian Jay. *Proceedings of the Royal Society B* 273: 701–706. doi:10.1098/rspb.2005.3373

EKANAYAKE, K.B., SUTHERLAND, D.R., DANN, P. & WESTON, M.A. 2015a. Out of sight but not out of mind: Corvids prey extensively on eggs of burrow-nesting penguins. *Wildlife Research* 42: 509–517. doi:10.1071/WR15108

EKANAYAKE, K.B., WESTON, M.A., DANN, P. & SUTHERLAND, D.R. 2016. Corvids congregate to breeding colonies of a burrow-nesting seabird. *Austral Ecology* 41: 291–301. doi:10.1111/aec.12311

EKANAYAKE, K.B., WESTON, M.A., NIMMO, D.G., MAGUIRE, G.S., ENDLER, J.A. & KÜPPER, C. 2015b. The bright incubate at night: Sexual dichromatism and adaptive incubation division in an open-nesting shorebird. *Proceedings of the Royal Society B* 282: 20143026. doi:10.1098/rspb.2014.3026

EKANAYAKE, K.B., WHISSON, D.A., TAN, L.X.L. & WESTON, M.A. 2015c. Intense predation of non-colonial, ground-nesting bird eggs by corvid and mammalian predators. *Wildlife Research* 42: 518–528. doi:10.1071/WR15080

GRIFFITHS, C.L. & RICHARDSON, C.A. 2006. Chemically induced predator avoidance behaviour in the burrowing bivalve *Macoma balthica*. *Journal of Experimental Marine Biology and Ecology* 331: 91–98. doi:10.1016/j.jembe.2005.10.002

HAFF, T.M. & MAGRATH, R.D. 2011. Calling at a cost: Elevated nestling calling attracts predators to active nests. *Biology Letters* 7: 493–495. doi:10.1098/rsbl.2010.1125

HAYWARD, J.L., ATKINS, G.J., REICHERT, A.A. & HENSON, S.M. 2015. Common Ravens (*Corvus corax*) prey on Rhinoceros Auklet (*Cerorhinca monocerata*) eggs, chicks, and possibly adults. *The Wilson Journal of Ornithology* 127: 336–339. doi:10.1676/wils-127-02-336-339.1

HENDERSON, L.A. & TRULIO, L.A. 2019. Can California Ground Squirrels reduce predation risk to Burrowing Owls? *Journal of Raptor Research* 53: 172–179. doi:10.3356/JRR-17-73

HIGGINS, P.J., PETER, J.M. & COWLING, S.J. (Eds.) 2006. *Handbook of Australian, New Zealand and Antarctic Birds*. Melbourne, Australia: Oxford University Press.

HUDSON, P.J. 1982. Nest site characteristics and breeding success in the Razorbill *Alca torda*. *Ibis* 124: 355–359. doi:10.1111/j.1474-919X.1982.tb03784.x

HUNT, G.R. 2000. Human–like, population–level specialization in the manufacture of pandanus tools by New Caledonian Crows *Corvus moneduloides*. *Proceedings of the Royal Society B* 267: 403–413. doi:10.1098/rspb.2000.1015

HUSBY, M. 2019. Nestling begging calls increase predation risk by corvids. *Animal Biology* 69: 137–155. doi:10.1163/15707563-20181058

IBM CORP. 2019. *IBM SPSS Statistics for Windows, Version 26.0.* Armonk, USA: IBM Corp.

JOLLES, J.W., OSTOJIĆ, L. & CLAYTON, N.S. 2013. Dominance, pair bonds and boldness determine social-foraging tactics in Rooks, *Corvus frugilegus*. *Animal Behaviour* 85: 1261–1269. doi:10.1016/j.anbehav.2013.03.013

LEIGHTON, P.A., HORROCKS, J.A. & KRAMER, D.L. 2009. How depth alters detection and capture of buried prey: Exploitation of sea turtle eggs by mongooses. *Behavioral Ecology* 20: 1299–1306. doi:10.1093/beheco/arp139

LIEBEZEIT, J.R. & GEORGE, T.L. 2002. *A summary of predation by corvids on Threatened and Endangered species in California and management recommendations to reduce corvid predation.* Species Conservation and Recovery Program Report, 2002-02. Sacramento, USA: California Department of Fish and Game.

LIMA, S.L. & DILL, L.M. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology* 68: 619–640. doi:10.1139/z90-092

MARCHANT, S. & HIGGINS, P.J. 1990. *Handbook of Australian, New Zealand and Antarctic Birds.* Melbourne, Australia: Oxford University Press.

MARZLUFF, J.M. 1988. Do Pinyon Jays alter nest placement based on prior experience? *Animal Behaviour* 36: 1–10. doi:10.1016/S0003-3472(88)80244-6

MARZLUFF, J.M., WALLS, J., CORNELL, H.N., WITHEY, J.C. & CRAIG, D.P. 2010. Lasting recognition of threatening people by wild American Crows. *Animal Behaviour* 79: 699–707. doi:10.1016/j.anbehav.2009.12.022

MASSARO, M., STARLING-WINDHOF, A., BRISKIE, J.V. & MARTIN, T.E. 2008. Introduced mammalian predators induce behavioural changes in parental care in an endemic New Zealand bird. *PLoS One* 3: e2331. doi:10.1371/journal.pone.0002331

MATSUI, H., HUNT, G.R., OBERHOFER, K. ET AL. 2016. Adaptive bill morphology for enhanced tool manipulation in New Caledonian Crows. *Scientific Reports* 6: 22776. doi:10.1038/srep22776

MCIVER, W.R., CARTER, H.R., HARVEY, A.L. ET AL. 2018. Avian and skunk predation of Ashy Storm-petrels at Santa Cruz Island, California. *Western North American Naturalist* 78: 421–440. doi:10.3398/064.078.0313

MINNAAR, C., BOYLES, J.G., MINNAAR, I.A., SOLE, C.L. & MCKECHNIE, A.E. 2015. Stacking the odds: Light pollution may shift the balance in an ancient predator-prey arms race. *Journal of Applied Ecology* 52: 522–531. doi:10.1111/1365-2664.12381

MYKYTOWYCZ, R., HESTERMAN, E.R. & PURCHASE, D. 1959. Predation on the wild rabbit by the Australian Raven. *Emu - Austral Ornithology* 59: 41–43. doi:10.1071/MU959041

NAKAZAWA, A. 2004. *The Behaviour of the Little Raven (*Corvus mellori*) and its Predation of Little Penguin (*Eudyptula minor*) Eggs on Phillip Island, Victoria.* Undergraduate thesis. St. Lucia, Australia: The University of Queensland.

PRINGLE, R.M., KARTZINEL, T.R., PALMER, T.M. ET AL. 2019. Predator-induced collapse of niche structure and species coexistence. *Nature* 570: 58–64. doi:10.1038/s41586-019-1264-6

PYKE, G.H., PULLIAM, H.R. & CHARNOV, E.L. 1977. Optimal foraging: A selective review of theory and tests. *The Quarterly Review of Biology* 52: 137–154. doi:10.1086/409852

RANGE, F., BUGNYAR, T., SCHLÖGL, C. & KOTRSCHAL, K. 2006. Individual and sex differences in learning abilities of ravens. *Behavioural Processes* 73: 100–106. doi:10.1016/j.beproc.2006.04.002

REGEHR, H.M., RODWAY, M.S. & MONTEVECCHI, W.A. 1998. Antipredator benefits of nest-site selection in Black-legged Kittiwakes. *Canadian Journal of Zoology* 76: 910–915. doi:10.1139/z98-016

REILLY, P.N. & CULLEN, J.M. 1981. The Little Penguin *Eudyptula minor* in Victoria, II: Breeding. *Emu - Austral Ornithology* 81: 1–19. doi:10.1071/MU9810001

RICHNER, H. 1989. Phenotypic correlates of dominance in Carrion Crows and their effects on access to food. *Animal Behaviour* 38: 606–612. doi:10.1016/S0003-3472(89)80005-3

ROCKWELL, C., GABRIEL, P.O. & BLACK, J.M. 2012. Bolder, older, and selective: Factors of individual-specific foraging behaviors in Steller's Jays. *Behavioral Ecology* 23: 676–683. doi:10.1093/beheco/ars015

ROWLEY, I. 1970. The genus *Corvus* (Aves: Corvidae) in Australia. *CSIRO Wildlife Research* 15: 27–71. doi:10.1071/CWR9700027

ROWLEY, I. 1973. The comparative ecology of Australian corvids. IV. Nesting and the rearing of young to independence. *CSIRO Wildlife Research* 18: 91–129. doi:10.1071/CWR9730091

ROWLEY, I. & VESTJENS, W.J.M. 1973. The comparative ecology of Australian corvids. V. Food. *CSIRO Wildlife Research* 18: 131–135. doi:10.1071/CWR9730131

SANTISTEBAN, L., SIEVING, K.E. & AVERY, M.L. 2002. Use of sensory cues by Fish Crows *Corvus ossifragus* preying on artificial bird nests. *Journal of Avian Biology* 33: 245–252. doi:10.1034/j.1600-048X.2002.330306.x

SAUNDERS, G.R., GENTLE, M.N. & DICKMAN, C.R. 2010. The impacts and management of foxes *Vulpes vulpes* in Australia. *Mammal Review* 40: 181–211. doi:10.1111/j.1365-2907.2010.00159.x

SCHOENER, T.W., SPILLER, D.A. & LOSOS, J.B. 2001. Predators increase the risk of catastrophic extinction of prey populations. *Nature* 412: 183–186. doi:10.1038/35084071

SHANNON, K., WESTON, M.A. & WHISSON, D.A. 2014. Sex bias in captured Little Raven *Corvus mellori* varies with entry aperture size in a modified Australian crow trap. *Corella* 38: 22–23.

SHINE, R. 2010. The ecological impact of invasive Cane Toads (*Bufo marinus*) in Australia. *The Quarterly Review of Biology* 85: 253–291. doi:10.1086/655116

STOKES, D.L. & BOERSMA, P.D. 1998. Nest-site characteristics and reproductive success in Magellanic Penguins (*Spheniscus magellanicus*). *The Auk* 115: 34–49. doi:10.2307/4089109

SUTHERLAND, D.R. & DANN, P. 2014. Population trends in a substantial colony of Little Penguins: Three independent measures over three decades. *Biodiversity and Conservation* 23: 241–250. doi:10.1007/s10531-013-0597-y

SWINBURNE, N. & JESSOP, R. 2005. Behaviour of the Little Raven *Corvus mellori* on Phillip Island, Victoria. *Australian Field Ornithology* 22: 137–145.

TAN, L.X.L., VAN DONGEN, W.F.D., SHERMAN, C.D.H. ET AL. 2021. Transmission of a novel predatory behaviour is not restricted to kin. *Biological Invasions* 23: 2473–2484. doi:10.1007/s10530-021-02517-4

TROSCIANKO, J., VON BAYERN, A.M.P., CHAPPELL, J., RUTZ, C. & MARTIN, G.R. 2012. Extreme binocular vision and a straight bill facilitate tool use in New Caledonian Crows. *Nature Communications* 3: 1110. doi:10.1038/ncomms2111

UETA, M. & HIRANO, T. 2006. Population decline of Japanese Lesser Sparrowhawks breeding in Tokyo and Utsunomiya, central Japan. *Ornithological Science* 5: 165–169. doi:10.2326/1347-0558(2006)5[165:PDOJLS]2.0.CO;2

UETA, M., KUROSAWA, R., HAMAO, S., KAWACHI, H. & HIGUCHI, H. 2003. Population change of Jungle Crows in Tokyo. *Global Environmental Research* 7: 131–137.

WARHAM, J. 1958. The nesting of the Little Penguin *Eudyptula minor*. *Ibis* 100: 605–616. doi:10.1111/j.1474-919X.1958.tb07963.x

WARREN, J.H. 1990. Role of burrows as refuges from subtidal predators of temperate Mangrove Crabs. *Marine Ecology Progress Series* 67: 295–299. doi:10.3354/meps067295

WIEBE, K.L., KOENIG, W.D. & MARTIN, K. 2007. Costs and benefits of nest reuse versus excavation in cavity-nesting birds. *Annales Zoologici Fennici* 44: 209–217. [Accessed at http://www.jstor.org/stable/23736733 in May 2021.]

YOUNG, E. 1994. *Skua and Penguin: Predator and Prey*. Cambridge, UK: Cambridge University Press. doi:10.1017/CBO9780511565311