



Cover, not caging, influences chronic physiological stress in a ground-nesting bird

Laura X. L. Tan, Katherine L. Buchanan, Grainne S. Maguire and Michael A. Weston

L. X. L. Tan, K. L. Buchanan and M. A. Weston (mwatson@deakin.edu.au), Deakin Centre of Integrative Ecology, School of Life and Environmental Sciences, Faculty of Science, Engineering and the Built Environment, Deakin Univ., c/- 221 Burwood Hwy, VIC 3125, Australia.
– G. S. Maguire, BirdLife Australia, Suite 2-05, The Green Building, 60 Leicester Street, Carlton, VIC 3052, Australia.

Predator exclosures ('nest cages') around nests are increasingly used to enhance hatching success of declining ground-nesting birds. However, such exclosures are contentious and have been suggested to have detrimental effects on the species which they aim to protect. This study examines whether exclosures increase physiological stress of incubating birds, a hitherto unrecognised and untested potential drawback of exclosures. Red-capped plover *Charadrius ruficapillus* hatching success was radically altered and significantly higher for nests with exclosures (96.2%) compared with those without (6.8%). Chronic physiological stress in parents (as measured by the heterophil/lymphocyte [H/L] ratio in blood) did not vary between nests with and without exclosures, or between the sexes. However the absence of vegetative cover at the nest site was associated with a 62.7% elevation in H/L ratio, indicating that incubating birds which place their nests in the open are subject to increased levels of chronic stress. The results from this study demonstrate the fundamental importance of predation for the nesting success of this species and confirm that chronic stress levels are not a detrimental side effect of exclosure use.

Depredation accounts for up to 80% of avian clutch failures across a variety of species, habitats, and geographic locations (Ricklefs 1969, Martin 1993), and the impacts of intense predation are especially evident among ground-nesting birds (Dowling and Weston 1999, Twyford et al. 2000, Dowling and Murphy 2001, Boland 2004). Anthropogenic processes (e.g. urbanisation) have contributed towards increased rates of clutch loss and declines in bird abundance (Marzluff 2001, Liebezeit et al. 2009, Cardilini et al. 2013), particularly where predators proliferate in disturbed or urbanised areas (Newton 2004, Voorbergen et al. 2012). Management approaches for problematic predators range from long-term solutions (e.g. habitat restoration or reintroduction of apex predators; Schmiegelow and Mönkkönen 2002, Letnic et al. 2012, Nifong and Silliman 2013, Ripple et al. 2013), to short-term solutions (e.g. repellents; Cox et al. 2004, Maguire et al. 2009) that may help sustain populations while longer-term solutions are sought or implemented. A common predator management strategy is to suppress populations of problematic predators (Robley et al. 2008, Roy et al. 2009, Smith et al. 2010). However, this is not universally successful and entire eradication of a predator population is rarely feasible (Schlaepfer et al. 2005, Roy et al. 2009). Another approach is to exclude predators from critical habitats at various scales. At a larger scale, this involves fencing predators out of critical habitat (Long and Robley 2004, Hayward and Kerley 2009, Weston et al. 2012). Under

specific circumstances, where particular species are suffering extreme predation during a vulnerable life history phase (e.g. the eggs of ground-nesting birds during the incubation period; Voorbergen et al. 2012, Burns et al. 2013), then a viable option may be predator exclusion on small spatial and temporal scales, using small-scale predator exclusion devices (e.g. around the nests of ground-nesting shorebirds; Supplementary material Appendix 1).

Nest cages ('predator exclosures') are designed to reduce or eliminate predator access to the nests of ground-nesting birds, but to permit access to the parents (Smith et al. 2011, Pearson et al. 2012). Such exclosures have attracted substantial research attention and uptake by managers (Supplementary material Appendix 1). Exclosures are usually wire, cage-like structures placed around an active nest (Niehaus et al. 2004, Isaksson et al. 2007). Exclosures have been applied to a number of ground-nesting bird species (mostly shorebirds), and studies report increased daily survival rates of eggs and improved hatching success (Supplementary material Appendix 1). However, limitations may offset any benefits conferred by exclosures (Isaksson et al. 2007, Hardy and Colwell 2008, Barber et al. 2010). To date, potential limitations identified include higher rates of clutch abandonment, independently or linked to, adult mortality (Hardy and Colwell 2008, Barber et al. 2010, Roche et al. 2010, Pearson et al. 2012). Adult mortality may be increased by exclosures because they facilitate predator ambush,

and perhaps reduce the speed or direction of adult escape (Niehaus et al. 2004, Isaksson et al. 2007). Likewise, brood survival may be reduced with the use of exclosures (Niehaus et al. 2004), because predator detection of nests may be facilitated by the presence of the exclosure and while the eggs cannot be accessed, the chicks become accessible post-hatching. The presence of natural cover and the size of the exclosure may also influence adult depredation, and mediates anti-predator response distances of the parents (Vaske et al. 1994, Murphy et al. 2003, Lomas et al. 2014). However, the potentially detrimental effects of exclosures remain to be thoroughly addressed. One possible drawback of using exclosures is that adult mortality (or reduced longevity) might conceivably occur if exclosures cause chronic physiological stress in incubating birds. We sought to test the possibility that exclosures may cause chronic physiological stress in incubating birds (a hitherto untested potential drawback of predator exclosures). Specifically, we investigate whether the placement of nest exclosures influences adult chronic physiological stress levels. We tested this contention as part of an assessment of the efficacy of predator exclosures on improving hatching success.

Methods

This study required a model species which suffers substantial egg depredation, and was a candidate for exclosure deployment (i.e. smaller than most of its egg predators, high nest tenacity and readily observable). The species selected was the red-capped plover *Charadrius ruficapillus*, a small ground-nesting shorebird widespread throughout wetlands in Australia, where it breeds from late July to late March (Marchant and Higgins 1993). This species is sexually dimorphic, and exhibits biparental incubation with the female incubating mostly during daylight hours, and males mostly nocturnally (Ekanayake et al. 2015). They nest both in the open and under cover (often live or dead vegetation), and choice of open and covered nests is abundant at the study site (Lomas et al. 2014). Previous data indicate low reproductive success, with the main cause being egg depredation by little ravens *Corvus mellori*, which are native to Australia, and red foxes *Vulpes vulpes*, which are an invasive species in Australia (Lomas et al. 2014). This study involved the use of exclosures on red-capped plover clutches at Cheetham Wetlands, Victoria, Australia (37°53'56"S, 144°47'33"E; ~420 ha), including adjacent Truganina Swamp (37°52'07"S, 144°48'12"E; ~148 ha) (for details see Antos et al. 2007). These locations are primarily closed to the public, host a natural and substantial population of breeding red-capped plovers (minimum counts exceed 200 birds), and was selected because previous studies report high predator abundances and high rates of clutch depredation (Lomas et al. 2014).

Predator exclosures

Ravens and foxes are the key predators of red-capped plover eggs at the study site (Lomas et al. 2014), and were the primary considerations for exclosure design. Exclosures were designed to be: 1) tall and wide enough to prevent predators from reaching in and rolling eggs out; 2) rigid

enough to resist predator attempts at gaining entry; 3) possess a meshed top to exclude avian predators and meshed sides to exclude mammalian predators; and 4) the aperture of the mesh needed to be small enough to prevent access by predators, but large enough to allow easy access to the nest by the parents. A circular design was adopted (after Mabee and Estelle 2000; Fig. 1). Exclosures were constructed with 3.15 mm thick wire, with four 6.3 mm stiffening rods for support. Exclosures stood 350 mm high and had a diameter of 800 mm. Aperture size was 50 mm wide by 100 mm tall. All exclosures were powder coated (Dulux™ 'Sandbank Matte') to help prevent corrosion, and to blend in with the substrate.

Experimental design

Intensive nest searches were conducted between late July 2012 and early March 2013, observing parental behaviour (e.g. alarm calling, flushing from nest) and identifying any nest scrapes. Upon discovery, nests were randomly assigned to one of two factor levels ('exclosure' or 'no exclosure' i.e. control). In order to reduce the risk of abandonment of clutches, the deployment of exclosures was avoided during laying (eggs were aged upon discovery using the flotation method; Liebezeit et al. 2007). Exclosures were placed on suitable clutches within 24 h of discovery (3.14 ± 1.01 h [mean \pm SE], 0.25–23.90 h), and removed if there were: 1) no egg(s) remaining, 2) no chicks in the exclosure (young leave the nest within hours of hatching, Marchant and Higgins 1993), or 3) if eggs were abandoned (i.e. two weeks had elapsed since the estimated hatch date, and no adult presence at the nest). At least three pegs were driven into the ground to secure exclosures to the substrate. Vegetation and the surrounding area was disturbed as little as possible.

Red-capped plover nests occur in the open and under varying degrees of vegetative cover and this influences the thermal environment in the nest and the distance at which anti-predator behavior is initiated by the incubating bird (Lomas et al. 2014). Nest cover (any vegetation dead or alive directly above the nest) was measured for each nest by placing a circular 10.5 cm diameter circle over the nest scrape,



Figure 1. Dimensions of a predator exclusion cage. The apertures outlined in white indicate three rows of the original 100 × 100 mm separated by a middle wire, creating apertures of 50 × 100 mm (50 × 50 mm in the top row). An incubating female red-capped plover can be seen in the exclosure.

and counting the number of 12×12 mm grids visible (88 grids in total) from directly above. The percentage of visible grids was calculated and a cover type ('cover' or 'no cover') allocated. A covered nest was defined as having $\geq 10\%$ of the grids covered (after Lomas et al. 2014).

To determine clutch fate, **targeted checks** of the nest were conducted using an estimated hatch date (Liebezeit et al. 2007) and **assuming a 30 d incubation period** (Lomas et al. 2014). Supplementary checks of the nest occurred **about once per week** and were made from a distance (i.e. whether a parent was observed incubating). Our checking protocols were designed to monitor cages for any obvious problems, and to determine if hatching occurred (i.e. our proximate measure of hatching success) while minimising visitation which may have resulted in incubator stress. Survival of eggs was defined as the eggs still being present in the nest, or the presence of nearby young, and 'hatching success' was defined as eggs hatching. **Where eggs disappeared before the estimated hatch date, depredation of eggs was assumed.** Claw marks, scats, or remains at the nest also helped identify the potential reason for the clutch loss.

Adults were captured using walk-in nest traps (Lomas et al. 2014), and trapping of females and males typically occurred during day and night, respectively (unpubl.). In order to reduce the risk of clutch abandonment, at least one egg from the adult's clutch had to be ≥ 10 d of age before attempting to trap a parent. Adults were measured, weighed, and fitted with the metal bands on the tarsus, and an orange plastic flag on the tibia (engraved with a unique two letter combination, placed on the tibia of the bird) which allowed individual identification from a distance. Birds had been flagged over the preceding four breeding seasons, and thus there were over 100 flagged birds present in the study sites. The mass (± 0.1 g) and tarsus plus toe (± 0.1 mm) measurements were recorded for each individual upon capture, and used to calculate the scaled mass index (SMI), following Peig and Green (2009). SMI provides an improved indication of the relative size of energy reserves of an individual animal (Peig and Green 2009), and was used in this study to index body condition.

Chronic stress causes the elevation of corticosterone, the principal avian stress hormone which serves to regulate a range of physiological processes including glucogenesis, metabolism, and behaviours associated with regulating adaptive behavioural changes (Wingfield 1994, Sapolsky et al. 2000). Elevations of baseline corticosterone can be difficult to measure due to the pulsatile release of corticosterone which makes field sampling problematic, due to the upregulation of corticosterone on capture. However, chronic stress can also be identified by other indices including changes in the peripheral blood cell population, as corticosterone causes a general down regulation of immune function (McEwen et al. 1997). This downregulation and redistribution of cells results in changes to the composition of the white blood cell community in a way which can be quantified (Gross and Siegel 1983). In order to examine any physiological stress imposed by exclosures on incubating birds, the ratio of heterophils to lymphocytes in blood ('H/L-ratio') was examined. The H/L-ratio has been demonstrated to be a reliable measure of chronic physiological stress in birds, where higher H/L

ratios reflect a higher level of stress (Gross and Siegel 1983, Jones et al. 1988). The H/L-ratio is a measure of chronic stress (Gross and Siegel 1983); therefore, stress induced by capture of the individual will not be reflected in the ratio. H/L ratio in birds may rise within 30 min–18 h after exposure to a stressor (Gross 1990, Mills et al. 1993, Davis 2005, Y. Rotman and M. Klassen pers. comm.); blood was sampled within 5–15 min of capture, and blood smears taken (Walberg 2001). All blood sampled birds had been exposed to their exclosure for more than 24 h before trapping.

All blood smears were stained using Geimsa stain (Sigma-Aldrich, Accustain® Wright-Giemsa stain, modified; ref WG16-500 mL, lot 109K4355). For each slide, 100 leukocytes were counted and classified according to cell type (heterophils, lymphocytes, basophils, eosinophils, and monocytes; after Gross and Siegel 1983). Cells were counted at $\times 100$ magnification under oil immersion. The number of heterophils and lymphocytes were then used to calculate the H/L ratio. Slides were counted blind to the status of the sample (sex or exclosure).

Statistical analysis

All analyses were performed using the statistical software package R 2.15.2 (R Development Core Team). Each nest was considered an independent data point for analysis. **Nests that had been flooded were excluded from all data analysis.** Summary statistics are presented as means \pm one standard error (unless otherwise stated).

Model selection was used to identify potential models with the greatest explanatory value based on the weights of the second order AIC (AICc) (Burnham and Anderson 2002). Here, candidate models are ranked from best to worst (low AIC weights represent better models). Δ AIC values of 0–2 indicate models which are considered to be strongly supported, and Δ AIC > 10 indicates little support for the model (Burnham and Anderson 2002). Where no clearly best model was generated, model averaging was undertaken (Burnham and Anderson 2002). The presence or absence of an exclosure on a nest was the focus of all models, however additional predictor variables were included where appropriate (Supplementary material Appendix 1).

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.0ms70>> (Tan et al. 2015).

Results

Seventy nests were located, excluding 18 nests that were either abandoned (83.3% of 18) or flooded (16.7%). Of these 70 nests, 26 (37.1%) were fitted with exclosures. Exclosures dramatically increased hatching rates; 96.2% of nests fitted with exclosures hatched at least one egg compared with only 6.8% of nests without exclosures. **Twenty-eight** (40.0%) of all nests had at least one egg hatch, with **25** (89.3%) of all **hatchings occurring in exclosures.** The remaining **42** (60.0%) were lost due to suspected depredation (eggs missing but not flooded before the hatching date, signs of egg shell or predator tracks); of these, only **one** (2.4%) was from a nest with an exclosure.

Table 1. The averaged general linear model of the influence of four variables on hatching success (hatch = 1, no hatch = 0): age of clutch at time of discovery from laying date (days), the presence (1) or absence (0) of an exclosure, time of year laid (Julian date), and the presence (1) or absence (0) of cover. Emboldened rows indicate significant results.

Variable	Co-efficient	Std error	z-value	p-value
Intercept	-4.536	2.133	-2.126	0.033
Age of clutch	0.124	0.074	1.687	0.092
Exclosure	6.580	1.537	4.280	0.000
Date	0.004	0.009	0.487	0.626
Cover	-0.516	0.920	-0.561	0.575

Other variables may influence the probability of clutches surviving to hatching (Supplementary material Appendix 2). Thus, a four variable general linear model with binomial distribution specified, model selection (using AIC_c) and model averaging procedure was undertaken to determine which, if any, variables may be associated with the probability of a clutch hatching (excluding nests that had been either abandoned or flooded) (Supplementary material Appendix 3). The average model explained 75.6% of the variation within the data (DF = 69, 65, null deviance = 94.22, residual deviance = 22.98 and AIC = 32.98, Table 1). **Exclosures were associated with a greater probability of hatching** (Table 1).

Physiological stress and body condition

Blood smears were taken from all adults during processing, with five samples being excluded from analysis due to uncertainty regarding attendance at a nest or because of previous sampling. Blood smears used in analysis were taken from 18 females and 14 males associated with nests with exclosures, and 9 females and 5 males captured from nests without exclosures.

A seven variable AIC_c general linear model selection with Gaussian distribution and model averaging procedure was undertaken to determine which, if any, variables may be associated with the H/L ratio (excluding nests that had been either abandoned or flooded) (Supplementary material Appendix 4).

While there appeared to be no significant relationship between the use of exclosures and H/L ratio ($C = 0.05$, $z = 0.24$, $p = 0.806$), a higher H/L ratio was evident in adults incubating at nests without cover (2.12 ± 0.21 [mean \pm SE], $0.69\text{--}4.44$) compared with those incubating at nests with cover (1.33 ± 0.14 , $0.52\text{--}2.79$; Table 2 and 3; Supplementary material Appendix 4). The average model explained 21.1% of the variation within the data (DF = 45, 38, null deviance = 50.6, residual deviance = 39.9 and AIC = 142.0, Table 3).

Table 2. The means and standard error of heterophils, eosophonils, basophils, lymphocytes, and monocytes counted per 100 leukocytes from blood smears taken from incubating adult red-capped plovers.

Predictor variable	n	Heterophils	Eosophonils	Basophils	Lymphocytes	Monocytes	H/L Ratio
With exclosure	32	58.000 ± 2.227	1.188 ± 0.231	0.938 ± 0.168	37.125 ± 2.092	2.750 ± 0.327	1.878 ± 0.192
Without exclosure	14	56.643 ± 3.503	1.214 ± 0.366	1.286 ± 0.370	37.786 ± 3.171	3.071 ± 0.450	1.779 ± 0.276
Female	27	57.926 ± 2.331	1.037 ± 0.264	0.741 ± 0.165	37.185 ± 2.216	3.111 ± 0.386	1.845 ± 0.196
Male	19	57.105 ± 3.129	1.421 ± 0.279	1.474 ± 0.290	37.526 ± 2.825	2.474 ± 0.319	1.852 ± 0.262
Cover present	16	51.625 ± 2.442	1.125 ± 0.340	1.000 ± 0.274	42.688 ± 2.610	3.563 ± 0.316	1.334 ± 0.143
Cover absent	30	60.767 ± 2.365	1.233 ± 0.238	1.067 ± 0.203	34.467 ± 2.100	2.467 ± 0.351	2.122 ± 0.212

Table 3. The averaged general linear model for the influence of seven variables on H/L ratio: the presence (1) or absence (0) of an exclosure; sex (female = 1, male = 0); scaled mass index (SMI); age of clutch at capture (days since laying), time of year laid (Julian date), and the presence (1) or absence (0) of cover. Emboldened rows indicate significant results.

Variable	Co-efficient	Std error	z-value	p-value
Intercept	3.145	2.164	1.453	0.146
Exclosure	0.050	0.202	0.245	0.806
Sex	-0.018	0.154	-0.118	0.906
Scaled mass index	-0.031	0.052	-0.585	0.559
Clutch age at capture	0.004	0.014	0.267	0.790
Date	0.000	0.002	0.115	0.908
Days between discovery and capture	-0.010	0.018	-0.555	0.579
Cover	-0.756	0.317	-2.387	0.017

Discussion

Exclosures significantly and substantially increased red-capped plover hatching success, in line with previous findings for other ground-nesting bird species including shorebirds (Supplementary material Appendix 1). Our study is the first to our knowledge to address the possible physiological effects of exclosures. We find no evidence that exclosures cause physiological stress (as measured by the H/L ratio), and in addition we find evidence that nesting cover may serve to reduce levels of stress in incubating birds.

Chronic physiological stress in incubating birds

The effect of exclosures on chronic physiological stress has not been previously investigated. We found no evidence for exclosure presence to be associated with elevated levels of physiological stress, and found that this conservation aid actually functions to increase hatching success. It is of course possible that our index of stress (H/L) is not sufficiently detailed or robust to detect the changes in individual condition. However, we think this to be unlikely, as numerous studies have confirmed the correlation of H/L with chronic stress in wild birds. Furthermore there was considerable variability between individuals in their H/L values. A second possibility is that samples were not taken at the right time to detect the increases in stress over time associated with exclosure placement. We also think this is unlikely, because although all samples used in analysis were from the first time a bird had been sampled during the season, there was no relationship between time since discovery of a nest and capture (and therefore time since exclosure placement) and H/L ratio within the exclosure group.

While exclosures were not associated with a higher H/L ratio (indicating a heightened level of stress), the absence of nest cover was. Aside from providing a form of concealment from visually searching predators (Götmark et al. 1995, Wiebe and Martin 1998), cover provides a more favourable thermal microclimate, which may consequently reduce thermal stress and alter thermoregulatory behaviour (Amat and Masero 2004a, Lomas et al. 2014). At Cheetham Wetlands, ground temperatures have been recorded to reach in excess of 50°C during the breeding season, and cover has been demonstrated to impart some thermal advantage to red-capped plover nests (Lomas et al. 2014).

A potential tradeoff for the protection provided by nesting under cover is an occluded view of surroundings, which may hinder the ability to detect approaching predators (Amat and Masero 2004b). The level of stress may influence flight initiation distance (Seltman et al. 2012), thought to be an important factor influencing adult mortality (Isaksson et al. 2007). The higher flight initiation distances generally seen in shorebirds with open nests (Amat and Masero 2004b) and in red-capped plovers nesting in the open (Lomas et al. 2014), may be associated with levels of stress as well as the greater predator detection distances afforded by the absence of cover. Conversely, obstructed views from the nest may reduce disturbance from neighbouring birds (Kim and Monaghan 2005), and potentially from predators; an 'ignorance is bliss' strategy may result in less observed stress. Birds, including red-capped plovers, sometimes alter nest locations on the basis of previous experience (Lima 2009, Self pers. comm.), and it is possible a poor experience at a covered nest (for example, a close encounter with a predator, or a series of clutch failures due to depredation of eggs), may stimulate these birds to nest in the open to take advantage of unobstructed vision and earlier predator detection. These poor past experiences may also be the cause of the higher H/L ratio observed. Cover may be associated with the occurrence of rodents, potential predators of eggs, young and adults, but we never recorded rodent predation.

The measure of nest cover used in this study is associated with differences in both the visibility from the nest and with the prevailing thermal environment (Lomas et al. 2014). We did not measure temperature or visibility directly during this study, partly to reduce disturbance at the nest, and note that cover is confounded with respect to its effect on both temperature and visibility from the nest. Thus, the exact mechanism by which chronic stress is elevated remains unclear and represents an interesting future study. Variation observed in H/L ratio in this study may also be related to other factors, such as environment or food restriction (Maxwell 1993), or innate immunity (Davis et al. 2004, Krams et al. 2012).

Chronic stress can detrimentally affect body condition (Vleck et al. 2000, Hórák et al. 2002, Masello et al. 2009). It may be that only the fittest birds can cope with the stress or thermal disadvantages of nesting in the open; however this study found no significant relationship between adult red-capped plover body condition and physiological stress (Table 3; Supplementary material Appendix 4). Female Kentish plovers *Charadrius alexandrinus* nesting under cover have previously been associated with having a poorer body condition, potentially due to being less able to cope with the higher ambient temperatures at exposed sites (Amat and

Masero 2004b). If fitter birds preferred to nest in the open this would suggest that greater field of view confers greater benefit than the thermal benefits provided by cover. This may explain why some birds nest in the open despite cover being available nearby.

Hatching success and the use of predator exclosures

Nests within exclosures produced 78.6% more chicks than those without. This was the highest rate of improvement in hatching success reported, compared with other species subject to exclosure deployments (3–67% increases in hatching success; $n = 13$ studies with comparable data; Supplementary material Appendix 1). Red-capped plover hatching success has typically been exceptionally low in previous years (36 nests; 13.3% successful hatches, 2010–2012), compared to 235 nests which failed to hatch (excluding 74 abandoned or flooded nests; unpubl.), so increases in hatching success may appear more pronounced when compared to other species that enjoy a higher rate of hatching success in general (Supplementary material Appendix 1). As red-capped plovers are a relatively small bird (Marchant and Higgins 1993), it was feasible to exclude larger key predators (little ravens and foxes) by using a smaller aperture.

In summary, we have shown that cover but not the use of exclosures mediated chronic adult stress in a plover. Future experiments could usefully disentangle the effects of thermal and predator environments on chronic adult stress. This could involve direct (but unobtrusive) quantification of these variables. Moreover, whether the elevated levels of chronic stress observed here influences adult longevity and reproductive fitness, warrants further investigation.

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Supplementary material (Appendix JAV-00625 at <www.avianbiology.org/readers/appendix>). Appendix 1–4.