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Case studies of motion-sensing cameras to study clutch survival and fate of real and artificial ground-nests in Australia

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ABSTRACT

Capsule: Trail cameras monitoring clutches of ground-nesting birds in Australia revealed survival rates and new causes of egg loss. We also show that nests with artificial eggs versus real eggs do not reveal the same information on predators.

Aims: We describe the application of trail cameras for monitoring real and artificial clutches of ground-nesting birds through a series of case studies. We rate the degree of inference used when defining nest outcomes and assigning fates.

Methods: Four case studies are presented, based on 326 deployments of cameras on real and artificial nests.

Results: The probability of hatching varied between species and populations (40.0–83.3% hatched), but not between urban and rural habitats. The ‘degree of inference’ scores did not differ between species and contexts. Two case studies which examined habitat-mediated survival (ecological hypotheses) found no difference in survival between urban and rural habitats, nor between open and covered microhabitats. Another case study (a management hypothesis) found that predator exclusion cages increased clutch survival even though predators sometimes breached the cages and cages altered the assemblage of predators visiting the area. A fourth study revealed that the assemblage of predators eating eggs differed between real and artificial nests.

Conclusion: Cameras enabled the survival and fate of most nests to be determined.

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In general, camera studies of bird nests have revealed a wealth of knowledge regarding nest success and causes of failure (DeGregorio *et al.* 2016). In recent years, there has been a proliferation of ecological studies which exploit the enhanced availability of cost-effective ‘trail cameras’ (De Bondi *et al.* 2010). Trail cameras represent a marked improvement in species detectability compared with previously available camera technologies (Dixon *et al.* 2009). Many of these cameras are motion-sensing, and can use infra-red to take images or video by day and night. To date, most applications of trail cameras have been to study mammals (e.g. McCain & Childs 2008, Harmsen *et al.* 2010, Morgan & Elliott 2011), even humans (Smith-Castro & Rodewald 2010). These cameras were developed to detect large and medium-sized mammals, and have been applied to a much more modest extent to birds. They have been used, for example, to assess prey of provisioning raptors (López-López & Urios 2010), breeding behaviour of vultures (Rollack *et al.* 2013), and document avian assemblages (Dinata *et al.*

2008, Stein *et al.* 2008) such as those exploiting carrion (Brown *et al.* 2015, Huijbers *et al.* 2015). In their review of the application of camera traps to ornithology, O’Brien & Kinnaird (2008) report only a handful of studies using these technologies for ‘clutch predation studies’, on real or artificial nests (see, e.g. Lomas *et al.* 2014). They also suggest trail cameras have the greatest promise for larger ground-dwelling birds.

Ground-dwelling birds, such as shorebirds, are considered especially vulnerable to egg depredation, which may suppress reproductive success to the extent that it represents a conservation concern (Dowling & Weston 1999, MacDonald & Bolton 2008). Indeed, shorebird populations are declining in Australia (Clemens *et al.* 2016) and elsewhere. In at least some ecosystems the most common outcome of a nest is that the eggs are eaten, and invasive predators and superabundant native predators are often suspected to be major egg predators of shorebirds and seabirds (Ekanayake *et al.* 2015a, 2015c). Outside Europe (MacDonald & Bolton 2008), little is known of the

survival or fate of ground-nesting bird clutches and the extent such egg predators play in clutch failure. What is known is derived from small-scale intensive studies often using repeat visits (Dowling & Weston 1999), constant (often slow frame-take-rate) video cameras (e.g. Demers & Robinson-Nilsen 2012, Ekanayake *et al.* 2015b), or broader citizen science schemes such as 'Nest Record Schemes' (e.g. Chambers *et al.* 2008). For many shorebird species, cryptic nest placement coupled with nest defence behaviours, that make the birds prone to disturbance, can mean that regular monitoring of nests has the potential to be harmful to egg viability (Martin & Geupel 1993). Moreover, at least some clutches hatch at night (H. K. Glover 2016, unpubl. data), meaning repeat visits may be unable to determine survival to hatching. Observers of nest fate often use inference based on evidence around the nest such as egg fragments or predator prints, and rarely directly observe the cause of nest mortality (Martin & Geupel 1993). The underlying modulators of nest success and fate remain poorly known for ground-nesting birds. The recent enhanced availability of remotely triggered day/night cameras has sparked a debate about their applicability and biases (O'Brien & Kinnaird 2008, McKinnon & Bêty 2009, Richardson *et al.* 2009) but they may have greater potential application in better understanding clutch success and fate for ground-nesting birds.

Here, we document applications of camera traps on real and experimental ('artificial') nests of small, medium-sized, and large shorebirds. Specifically, we describe the determination of survival to hatching and causes of failure, for a group of species for which clutch survival and fate is poorly or entirely unknown. The purpose of this paper is to describe the application of cameras in this context, with a view to exploring some of the strengths and weaknesses of using trail cameras for this purpose. The vast majority of the data we present has not been published elsewhere, and success or fate of shorebirds breeding in Australia is poorly known.

Case studies

A series of case studies were selected to demonstrate a range of potential applications of cameras to study the survival and fate of ground-nesting bird clutches. These studies were conducted as part of a broader effort to understand patterns of clutch survival and fate in Australian shorebirds (e.g. Cardilini *et al.* 2013, Ekanayake *et al.* 2015a, 2015b, 2015c). The case studies also represent the best available account of clutch

survival and fate yet available for the shorebird species studied. The case studies deal with:

- (1) Habitat-mediated clutch success at two scales:
 - (a) At a larger scale, we examine whether clutch survival varies between urban and rural habitats. The rural areas studied were typical of Australian rural zones, and often involve extensive rather than intensive agricultural areas, distinctly separate from nearby centres such as towns or cities (after Australian Institute of Health and Welfare 2014). Urban habitats are one of the most rapidly expanding habitats in the world, and previous studies suggest that, in many species-place permutations, reproductive success is lower in urban areas (Marzluff 2001). This is not universal, however, and other studies find no difference or higher reproductive success in urban environments (Gilbert 1989, Kamp *et al.* 2015, Marzluff 2001, Cardilini *et al.* 2013). Based on the general pattern reported, we expect that non-urban habitats will be associated with higher hatching success.
 - (b) We examine whether microhabitat influences clutch survival or outcomes. At this scale, birds inhabiting microhabitat mosaics face choices regarding the types of microhabitats in which to nest. For example, in wetlands, shorebirds may choose between open and covered nest sites (i.e. those under vegetation). Microhabitats and nest localities can harbour different risks (e.g. Gómez-Serrano & López-López 2014). Covered nests may buffer against disturbance-associated responses but enable predators to approach closely, potentially compromising nest crypsis as the departing parent inadvertently reveals the nest location (Gómez-Serrano & López-López 2014, Lomas *et al.* 2014). Covered clutches may be more prone to depredation because many potential egg predators are largely confined to structurally complex habitats (e.g. rodents and reptiles; Brown *et al.* 2011, Schlinkert *et al.* 2016). Specifically, we expect that, given birds nest in cover and in the open (i.e. an evolutionarily stable strategy), hatching success should be similar between microhabitats but prevailing fates might differ.
- (2) Management studies which test management interventions to enable more effective conservation approaches. We examine the effectiveness of

predator exclosures around shorebird nests (Tan *et al.* 2015). Predator exclusion cages on nests may prevent or reduce egg loss to predators, provided that the cages effectively exclude egg predators, most of which have larger body sizes than the species to be protected (Smith *et al.* 2011). Controversy exists on their effectiveness *per se*, and potential disadvantages render the efficacy of cages ambiguous. One key potential disadvantage, that cages attract more or a different assemblage of predators, remains an important but unanswered question which has received scant attention (Mabee & Estelle 2000). We address these questions here.

- (3) Methodological comparisons regarding artificial versus real nests have been addressed commonly in the literature (e.g. Major & Kendal 1996), and many but not all studies report that artificial nests do not represent effective indices of real nest survival and fate (Major & Kendal 1996, DeGregorio *et al.* 2016). We conduct a case study on comparing artificial and real shorebird nests in a coastal environment, recognising that previous assessments focus on terrestrial rather than open coastal ecosystems (GoogleScholar search, 10 August 2017, using keywords 'artificial nest', revealed 21 studies comparing real and artificial nest survival, of which two only were coastal, and only 1 involved the ground nests of shorebirds [Nguyen *et al.* 2006]). Specifically, we compare the predator assemblages attracted to real versus artificial clutches.

Methods

Real nest searching involved careful, systematic searching, by car or foot. All artificial clutches were at least 100 m from any other artificial or real nest and usually greater than 200 m from any contemporaneously deployed artificial clutch or active real nest, as is standard practice (Maguire *et al.* 2009). Placement of artificial nests involved generating random points constrained by spacing requirements. The points were adjusted by a maximum of 20 m (while still maintaining required separation) in the field to ensure that the randomly allocated treatment criteria were met (e.g. that a nest allocated to the factor-level 'cover' was in realistic cover used by the study species). Red-capped Plovers that select covered nest microhabitats, always nest under vegetation such that the incubator can move quickly to and from an open area (M.A. Weston 2017, unpubl. data), thus

visually foraging predators can still sight clutches as they move around open areas near fringing vegetation. Specifically, cover at real Red-capped Plover nests can be assessed by recording the number of grids obscured (NGO) on a small white disk in the nest, when viewed from above (Lomas *et al.* 2014). This reveals a bimodal distribution of cover, with one mode being 'open' nests with 0–11% NGO and a second mode being 'covered', 91–100% NGO (Lomas *et al.* 2014). In this study, artificial nests replicated these modes, that is, had 0% NGO (open) or 100% NGO (covered).

We used two models of digital Scoutguard™ scouting/trail camera (HCO outdoor products): KG-680 V and DTC-530 V. Remotely triggered trail cameras, unlike most dedicated video camera systems (e.g. Ekanayake *et al.* 2015b), can monitor continuously for lengthy periods (even if set to video), do not involve cables running to and from the camera, and involve less post-field processing time because data are stored as separate files. The basic configuration was to install a single camera cryptically, on a low stake, 1–3 m from a nest, such that it had as clear a view of the nest as possible, to avoid false triggering, while itself being hidden by nearby cover such as bushes or logs, where possible (cameras on beaches were often in the open). Cameras were positioned within modified, unused, plastic food containers painted to maximize local camouflage and to improve weather resistance. In this study, cameras were generally set to maximum sensitivity, the minimum interval between triggers, and to take three still images. Cameras monitoring false nests as part of the predator exclusion experiment were set to record video. Cameras were periodically checked, and removed if the eggs had disappeared; most checks were from a distance, with occasional checks of battery and memory status (maximum of four checks in 30 days). Thus, settings and checking intervals were consistent between projects, and the camera models were largely equivalent in terms of sensors and flashes, and were never confounded within projects.

Cameras were installed only by trained personnel, in the absence of predators, and as rapidly as possible. Real nests were generally not revisited (i.e. cameras were not checked) until estimated hatch date (estimated using the flotation method, Liebezeit *et al.* 2007), unless clutch loss was determined from a distance or based on adult absence. To avoid potential nest abandonment, we never deployed cameras on nests where laying was underway. For artificial clutches, visits were made at pre-determined experimental intervals (≥ 7 days).

The study populations are described in Table 1 (species are described in Marchant & Higgins 1993).

Table 1. Study populations and hatching success. The raw percentage of clutches that hatched, and those for which hatching could not be determined are shown. Additionally, for real nests, the results of univariate logistic Generalized Linear Models of hatching or non-hatching (excluding nests for which fate could not be determined or days to hatching at camera deployment was not available) are also presented. 'Source' refers to descriptions of study populations. The significant *P* value is in bold. Size information is from Menkhurst *et al.* (2017).

Species (bill length mm; wing length mm; mass g)	Population (range of latitudes/longitudes/centroid of study area)	Deployment dates; species breeding habitats ^a	Source: methods and study area	Sample size: number of nests (number in model)	Hatched (%)	Unknown (%)	Model coefficient (days to hatching at day of camera deployment) (\pm se)	Z value	<i>P</i>	<i>R</i> ²	df
Masked Lapwing (30–36; 236–259; 214–302)	Tropical. Mackay region, North Queensland (21° 04'11"S, 149°12'05"E)	16/04/2011–7/12/2016; Open areas with low vegetation, e.g. gardens, grasslands, wetland margins	N/A	31 (23)	64.5	16.1	−0.13 \pm 0.08	−1.68	0.094	0.14	21
Masked Lapwing (32–40; 213–236; 297–425)	Temperate. Phillip Island, Victoria ^b (38°28'32"S, 145° 12'12"E)	9/05/2010–13/08/2010; Open areas with low vegetation e.g. gardens, paddocks, wetland margins	Cardilini <i>et al.</i> (2013)	32 (32)	71.9	0.0	−0.21 \pm 0.07	−2.88	0.004	0.37	30
Hooded Plover (16–19; 138–149; 79–110)	Temperate coastal. Victorian Coast (142°02'43"E–146° 18'19"E)	9/10/2009–23/02/2016; Eastern population breed on sandy beaches and dunes on surf beaches	Mead (2012)	95 (75)	40.0	8.4	0.02 \pm 0.03	0.67	0.504	0.01	73
Bush Stone-curlew (45–53; 260–310; 530–860)	Tropical. Mackay region, North Queensland (21° 04'11"S, 149°12'05"E)	13/01/2011–7/12/2011; Woodlands with sparse understory, parks and gardens.	N/A	18 (16)	83.3	5.6	0.07 \pm 0.17	0.40	0.686	0.01	14
Beach Stone-curlew (70–82; 272–298; 870–1130)	Tropical. Mackay region, North Queensland ^c	Sandy, muddy and pebble shores	N/A	1	100	0	N/A	N/A	N/A	N/A	N/A
Artificial Red-capped Plover nests (caged vs. uncaged) (13–15; 126–136; 30–46)	Temperate, near-coastal. Western Treatment Complex, Werribee (38° 00'00"S, 144°34'00"E)	1/08/2016; Species breeds on coasts, in near-coastal and inland wetland margins	Tan (2012); wetland which is also a working waste-water treatment plant	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Artificial Hooded Plover nests (as above)	Temperate. Victorian coasts within breeding distribution (as above)	4/09/2011–14/09/2011; Placed in potential habitat in dunes during the breeding season	Cribbin (2012); high energy coasts of western and central Victoria	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A

^aAll sites had few people apart from the urban treatment sites.

^bPhillip Island is virtually free of Red Foxes *Vulpes vulpes*.

^cLocation withheld.

To calculate ‘estimated days to hatching’ we used estimates of incubation periods of Bush Stone-curlew (*Burhinus grallarius*; 30 days, breeds June–December), Masked Lapwing (*Vanellus miles*; 31 days, May–September), and Hooded Plover (*Thinornis rubricollis*; 28 days, September–March) (Marchant & Higgins 1993). Artificial clutches, placed in artificial nests, consisted of two (three when mimicking Hooded Plover) Japanese Quail (*Coturnix coturnix japonica*) eggs placed in a small scrape in the substrate which mimicked real Hooded or Red-capped Plover *Charadrius ruficapillus* nests. Henceforth, these are referred to as model eggs.

Cameras generate sequences of time and date-coded images or videos. Some of these images may provide unambiguous evidence of clutch fate such as a predator

eating or removing an egg or newly hatched chicks sitting in a nest (Figure 1). However, the images may omit direct evidence of this kind, instead providing circumstantial but strong evidence of eggs being taken; for example, one image may show a presumed predator standing near the eggs, and the next image may show the eggs are no longer present. In the case of crushing (mechanical destruction), inference is often required as the location of the eggs may be difficult to ascertain following disturbance of the site (Figure 2). These situations are examples of many potential scenarios where some degree of inference is required to interpret the photographic record. We developed an *a priori* scale specifically for camera studies of nests (Table 2) and coded the degree of inference required to assign fate to each nest studied.

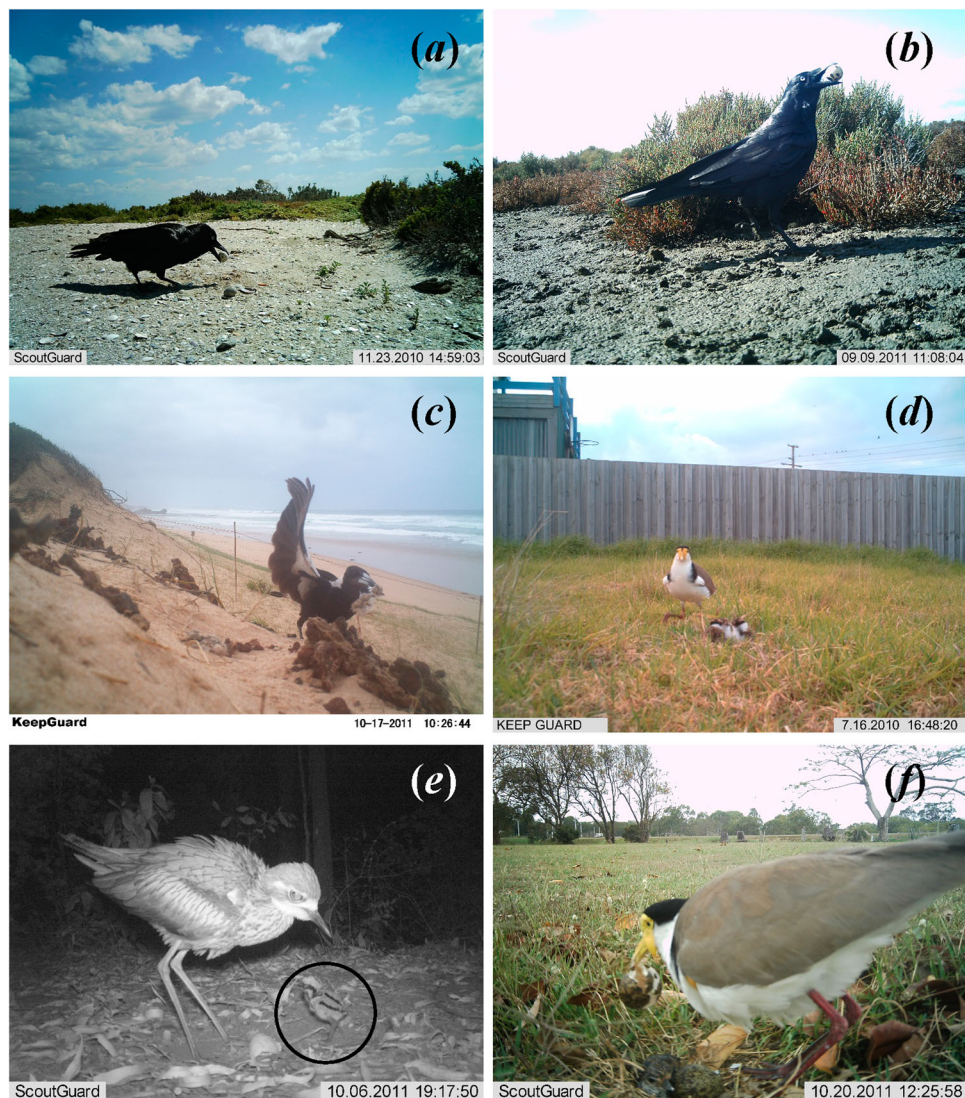


Figure 1. Unambiguous evidence of clutch fate as revealed by trail cameras positioned by shorebird nests: (a) and (b) Little Raven preying on Red-capped Plover eggs; (c) Australian Magpie preying on a newly hatched Hooded Plover chick; (d) newly hatched Masked Lapwing chicks sitting in the nest; (e) newly hatched Bush Stone-curlew chick (encircled) with adult; and (f) newly hatched Masked Lapwing chick sitting on nest while adult removes egg shell remains.

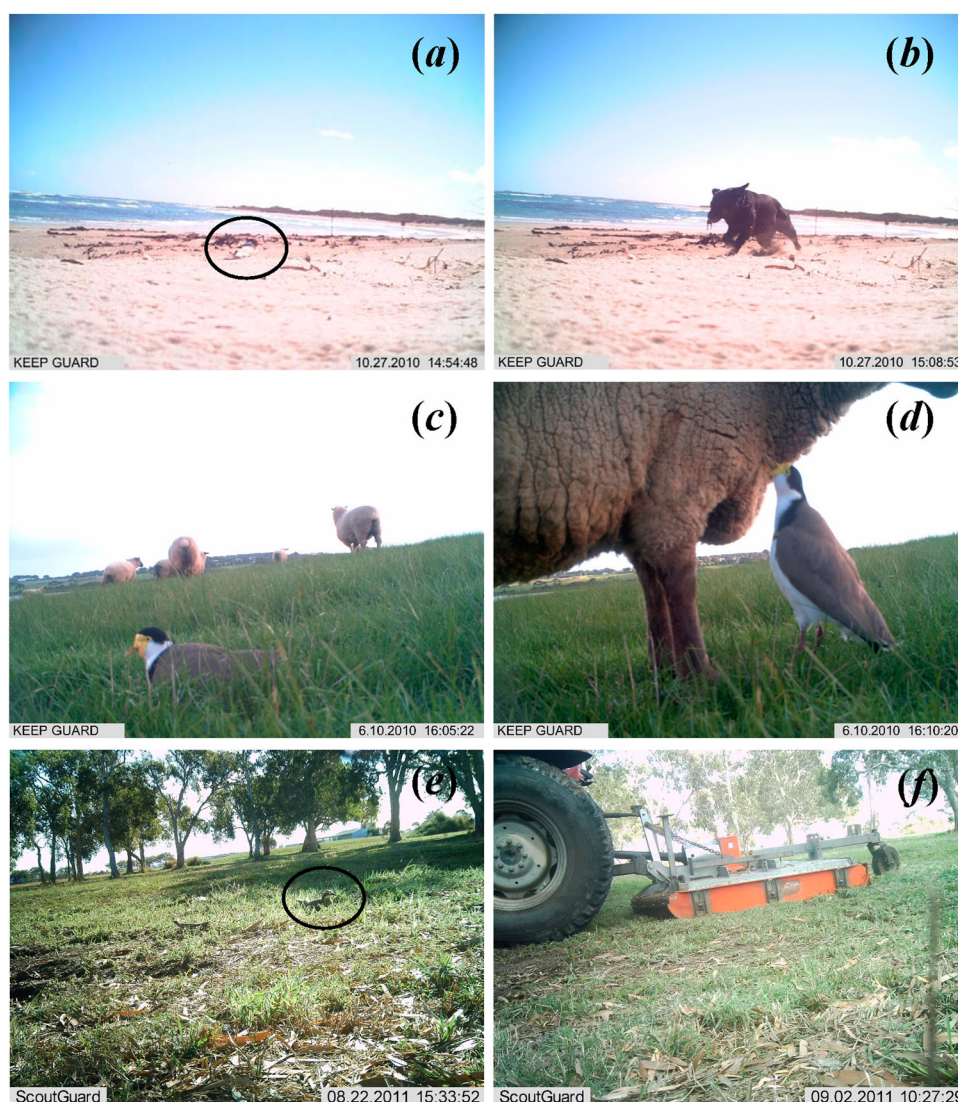


Figure 2. Selected images showing inferred crushing of eggs: (a) and (b) are a sequence of Hooded Plover (encircled) sitting on nest and eggs being crushed by a dog; (c) and (d) Masked Lapwing sitting on nest and eggs being crushed by a sheep; (e) and (f) Bush Stone-curlew sitting on nest (encircled) and eggs being crushed by a tractor mounted slasher.

Case studies

The case study designs are described in Table 3.

Statistical analysis

'Days to fate' is the number of days between camera deployment to failure and hatching of a clutch. For real nests if one or more chicks hatched then the clutch was considered successful, if no chicks hatched then the clutch was considered to have failed. When examining hatching success, the duration over which a clutch has been extant (i.e. 'exposed' to the risk of loss, the inverse of the time required to survive to hatching) at the time of discovery needs to be considered

(Mayfield 1961). We estimated the number of days to hatching of a clutch at discovery as described above, and used that as a covariate in models to adjust for exposure.

Analyses are specified below (Tables 1 and 3). Analyses including generalized linear models (GLM), one-way analysis of similarity (ANOSIM), similarity percentages (SIMPER) and *t*-tests were performed in R (version 3.1.2; <http://cran.r-project.org>) using 'glm', 'anosim', 'simper' within the base packages and package 'vegan'. The graph presents raw untransformed data to enhance readability and does not imply normality of data. Summary statistics are presented as means \pm 1 standard error (se) (unless otherwise stated) and model statistics include coefficients, se, *Z* and *P* values.

Table 2. A coding system for the degree of inference used to interpret camera data to assign clutch fate in shorebirds. Code 1 (the middle value) was rarely used but is presented here for completeness. The two-point scale was 0 (low degree of inference required) and 1 (inference required and/or circumstantial evidence available).

Code with three-point scale (% of nests)	Code with two-point scale (% of nests)	Depredated	Abandoned	Hatched
0 (65.3)	0 (65.3)	Event captured fully, e.g. egg in predators mouth, or, head of predator in nest	Camera detects change from incubation to parental absence, e.g. adults cease being detected in images but the eggs remain visible	Images of chicks in or near nest site
1 (6.7)	1 (34.7)	Predator seen in images in the vicinity of the nest close to the time the eggs disappeared, but not sighted preying on eggs	N/A	Images of adult brooding or images of chicks in the distance
2 (28.0)	1 (as above)	Eggs discovered missing, no evidence on camera	No evidence, but eggs discovered cold and unattended	No images of chicks, but chicks discovered on visitation

Table 3. Design of the case studies analysed in this paper. ML: Masked Lapwing (Northern or Southern); BSC: Bush Stone-curlew; RCP: Red-capped Plover; (A): artificial.

Case study	Comparisons: sample sizes and deployment dates by treatment and population	Predictions	Analysis (link function/resemblance matrix), response variable (R) and predictors (P)	Comments
1. <i>Urban versus rural clutch success.</i> An example of clutch success variation with habitat (larger scale). Real nests	ML(N): urban (24: 11/08/2011–7/12/2011) vs. rural (7: 16/04/2011–29/10/2011) ML(S): urban (13: 9/06/2010–26/08/2010) vs. rural (19: 9/05/2010–13/07/2010) BSC: urban (8: 13/01/2011–12/10/2011) vs. rural (11: 13/01/2011–12/10/2011)	Urban hatching success will be lower than rural hatching success for all systems	GLM R = Hatching success; P = Habitat type, days to hatching Binomial distribution	
2. <i>Microhabitats and artificial clutch survival.</i> An example of clutch variation of success with microhabitat	A: cover (17: 08/09/2011–09/09/2011) vs. open (16: 08/09/2011–09/09/2011)	Covered nests will exhibit similar survival compared with open nests (as most predators are visual foragers)	GLM R = Days to fate; P = Habitat type Gaussian distribution	Two Quail eggs per nest mimicking Red-capped Plover nests at Cheetham Wetlands and Truganina Swamp, Melbourne (see Antos <i>et al.</i> 2007, Lomas <i>et al.</i> 2014). Days to fate: 1.5 ± 0.7
3. <i>Predator exclusion cages and artificial clutches.</i> An example of examining the possible merits and drawbacks of a conservation intervention. Artificial nests ^a	A: caged (17: 01/08/2012–01/08/2012) vs. uncaged (32: 01/08/2012–01/08/2012); Total 70 nests, 17.4% unknown fate; 27.5% 'survived' 28 days	Caged clutches will exhibit higher survival than uncaged nests	GLM R = Days to Fate; P = Habitat type Gaussian distribution	Two Quail eggs per nest mimicking Red-capped Plover nests at Western Treatment Complex, Werribee, Melbourne (see Tan 2012). Days to fate: 8.4 ± 0.8
	A: cage (17: 01/08/2012–01/08/2012) vs. uncaged (21: 01/08/2012–01/08/2012)	Caged clutches will attract a higher and different diversity of predators as the presence of a cage will provide an additional visual cue	ANOSIM (zero-inflated Bray-Curtis dissimilarity matrix) and SIMPER R = Predator (0/1); P = Treatment (caged vs. uncaged)	Two Quail eggs per nest mimicking Red-capped Plover nests at Western Treatment Complex, Werribee, Melbourne (see Tan 2012)
4. <i>Real versus artificial nests.</i> A methodological question assessing the utility of artificial nests as an index of real nest survival or fate	HP: artificial (23: 04/09/2011–13/09/2011) vs. real (29: 02/09/2011–20/02/2012)	Real nests will attract a higher and different diversity of predators as the presence of an incubator will provide more visual and olfactory cues	ANOSIM (zero-inflated Bray-Curtis dissimilarity matrix) and SIMPER R = Predator; P = Treatment (real vs. artificial)	Artificial nests in the same habitat (dunes); three Quail eggs per nest mimicking modal clutch size of Hooded Plover (see Mead 2012 and Cribbin 2012)

^aSample sizes represent the suitable data analysed from a balanced design involving 35 caged and 35 uncaged nests.

Results

Results are derived from 326 camera deployments. Of these, we deployed 150 cameras on artificial clutches.

Deployments which resulted in the loss of cameras due to flooding and theft are omitted.

Table 4. Fate categories recorded and the frequency they occurred for each population or experiment.

Fate	Bush Stone-curlew (real)	Hooded Plover (real)	Hooded Plover (artificial)	Masked Lapwing (real; Phillip Island)	Masked Lapwing (real; Mackay)	Red-capped Plover (artificial; caged-uncaged)	Red-capped Plover (artificial; open-closed)	Total
Hatch	15	38	N/A	23	20	N/A	N/A	96
Corvid	0	10	17	0	0	23	32	82
Unknown (predator) ^a	1	0	22	0	0	12	3	38
Survived	0	0	0	0	0	19	0	19
Unknown	1	8	0	0	5	0	0	14
Red Fox	0	11	1	0	0	1	0	13
Swamp Harrier	0	1	0	1	0	10	0	12
Non-hatching ^b	0	2	N/A	1	5	N/A	N/A	8
Flood (tide)	0	8	0	0	0	0	0	8
Australian Magpie	0	6	0	0	0	2	0	8
Abandoned	0	3	N/A	4	0	N/A	N/A	7
Unknown rodent	0	0	4	0	0	0	0	4
Unknown (did not hatch) ^c	0	4	N/A	0	0	N/A	N/A	4
Human ^d	0	1	0	1	0	0	1	3
Buff-banded Rail	0	0	0	0	0	2	0	2
Flood (fresh water)	0	1	0	0	0	0	0	1
Australian Brush Turkey <i>Alectura lathamii</i>	1	0	0	0	0	0	0	1
Dog <i>Canis familiaris</i>	0	0	1	0	0	0	0	1
Nankeen Kestrel	0	1	0	0	0	0	0	1
Brushtail Possum <i>Trichosurus vulpecula</i>	0	0	0	1	0	0	0	1
Sheep <i>Ovis aries</i>	0	0	0	1	0	0	0	1
Purple Swamp Hen <i>Porphyrio porphyrio</i>	0	0	0	0	1	0	0	1
Water Rat <i>Hydromys chrysogaster</i>	0	1	0	0	0	0	0	1

^aEggs preyed upon but identity of predator not known.^bEggs present but did not hatch.^cCause of failure unknown but eggs known not to hatch.^dFailed due to direct human interference such as egg removal or destruction.

Real clutch survival

Four shorebird populations had sufficient camera deployments to determine hatching success (176 nests of which 158 were associated with an estimate of days to hatching). In order to examine hatching success given the duration of camera monitoring, we analysed whether a clutch hatched (binomial distribution) using a GLM with estimated days to hatching at deployment as a predictor variable. In terms of survival, the raw percentages of clutches hatching was rather high but varied between populations substantially (40.0–83.3%; Table 1). While most nests were clearly determined to have hatched or failed to do so, some camera deployments failed to reveal whether a nest had hatched (Table 1). GLMs indicated that, for one population only, age of the clutch at deployment day (i.e. days to hatching) negatively influenced the probability of a nest hatching (i.e. the more days to hatching the lower the probability of hatching), with a tendency for the same effect in another population of the same species (Table 1).

Fate and inference

None of the nests we studied were assigned a fate by direct observation, that is, without the use of cameras. Twenty-three fate types were recorded from the 326 nests monitored and egg predators were the overwhelming cause of clutch failure (Table 4). While cameras were extremely helpful, revealing many hitherto unknown fate types, they did not always unambiguously identify the fate of a clutch, and often (34.7%) some degree of inference was required to assign a fate. In our three-point 'degree of inference' scale (Table 2), the middle value was rarely used (6.7%), and so we converted this to the two-point (binary) scale (0 involved a low degree of inference required, 1 required inference or involved circumstantial evidence). In order to assess whether the degree of inference differed between camera projects, a GLM, featuring Bush Stone-curlew as a reference variable, was conducted. This revealed that the degree of inference did not differ between nests of Bush Stone-curlew, Hooded Plover, and Masked Lapwing (Table 5).

Table 5. Summary of GLM testing degree of inference by species. Bush Stone-curlew was the reference species.

Response variable (<i>N</i> = 176)	Predictor	Estimate	se	Z value	<i>P</i>
Inference	Intercept	0.693	0.500	1.386	0.166
$R^2 = 0.003$	Hooded Plover	0.179	0.548	0.327	0.744
df = 173	Masked Lapwing	-0.071	0.566	-0.125	0.901

Incidental observations

The cameras detected many instances of interesting or unrecorded aspects of parental behaviour such as parental defence or care (Figure 3). Additionally, in some colour-marked populations, the cameras were able to determine the identity of individual adults (Figure 4).

Case study 1: urban versus rural clutch success

Urban sites were primarily residential areas with high densities of houses, whereas rural areas were primarily agricultural land with low densities of houses. Three shorebird populations which were readily classified as breeding in urban or rural habitats were considered (Table 6). While age of the clutch at day of camera deployment significantly influenced the probability of hatching for Masked Lapwing on Phillip Island, none of the species we examined showed a systematic difference in the probability of hatching between habitats, as revealed by camera data (Table 6). Too few known fate types other than hatching were available to enable multivariate comparisons of predator assemblages in urban versus rural habitats for any of the three study populations.

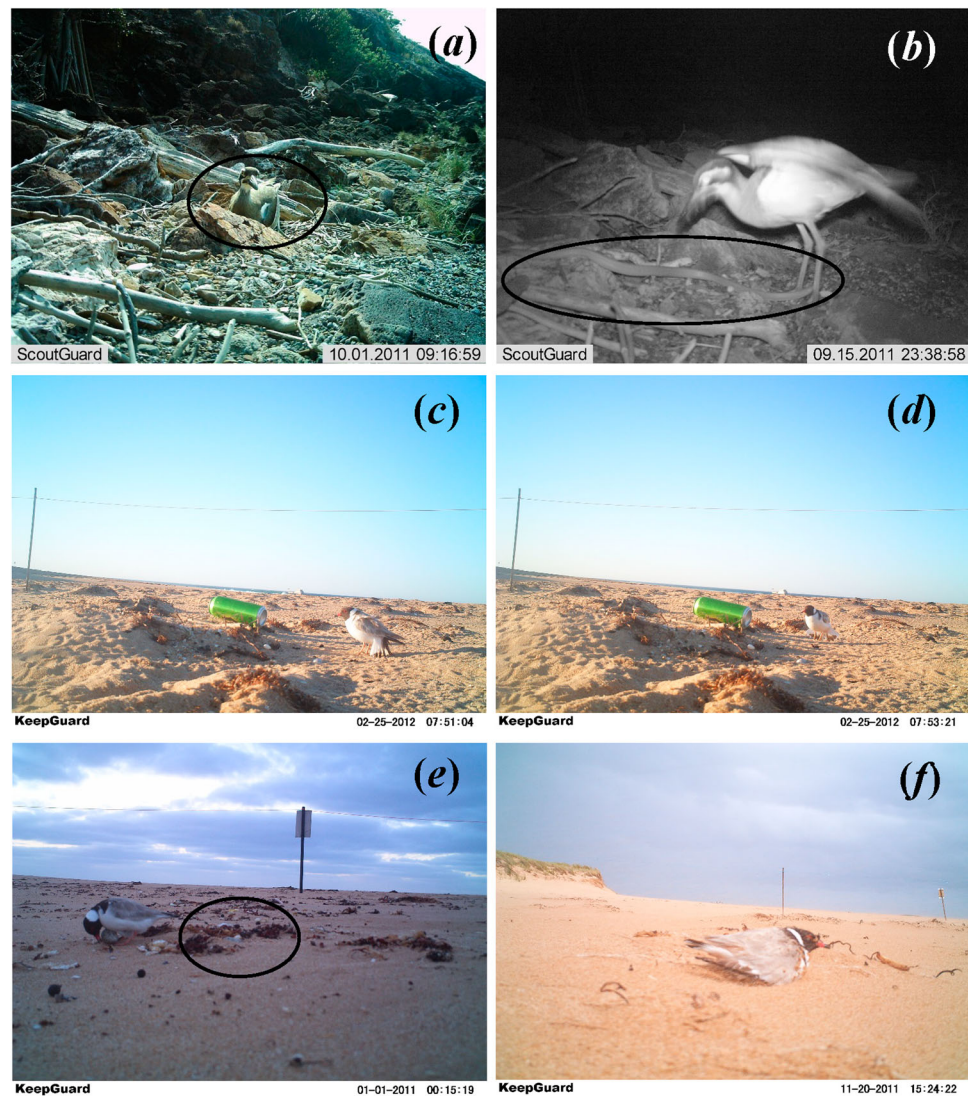


Figure 3. Selected images showing hitherto unreported aspects of parental care: (a) and (b) Beach Stone-curlew (encircled) successfully defending its nest from a snake (encircled); (c) and (d) Hooded Plover performing an aggressive display towards litter; (e) Hooded Plover rolling displaced egg back into nest (encircled); and (f) Hooded Plover persisting with incubation in windy conditions.

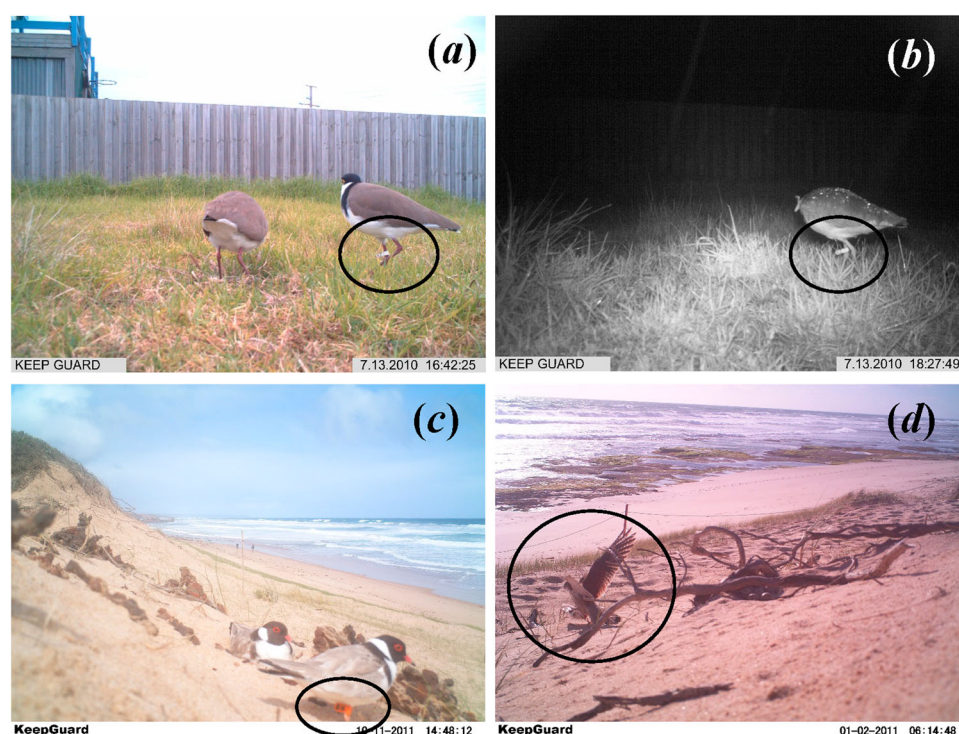


Figure 4. Examples of images in which adult identity was determined by reading the individual flag markings on the leg (flags are encircled and easily read using the zoom tool): (a) marked Masked Lapwing during daytime; (b) marked Masked Lapwing at night; (c) marked Hooded Plover during daytime; and (d) marked Hooded Plover being attacked by a Nankeen Kestrel *Falco cenchroides*.

Case study 2: microhabitats and artificial clutch survival

Red-capped Plovers nest both under cover and in the open and therefore represent an ideal system in which to test relevant hypotheses. We examined whether vegetative cover above a nest conferred an anti-predator advantage compared with clutches in the open using artificial clutches ($n = 33$ nests; Table 3). A GLM revealed no difference between covered and non-covered nests in terms of survival (Table 7). Corvids were the predominant cause of failure in both covered and open microhabitats (all but one known non-hatching fate type), so we did not investigate the assemblages of clutch fates further.

Case study 3: predator exclusion cages and artificial clutches

A study of predator exclusion cages on artificial nests (mimicking Red-capped Plover nests) revealed that the use of an exclusion cage increased clutch survival; a GLM specifying binomial distribution (survived = 0, did not survive = 1) of the influence of the presence or absence of an exclusion cage on survival of artificial nests and eggs to 28 days (Table 7, Figure 5; the low R^2 suggests that other factors may influence survival). While exclusion cages conferred a significant benefit to

clutch survival, some predators were still able to access model clutches within cages. Seventeen (48.6%) clutches with exclusion cages did not survive 28 days and 33 (94.3%) clutches without cages did not survive 28 days. Predators of clutches with exclusion cages were primarily Little Raven *Corvus mellori* (82.4%) but a Buff-banded Rail *Gallirallus philippensis* (5.9%) also took eggs from within a cage. These predators moved freely through the cage or squeezed through the 10×10 cm mesh, prompting us to reduce the aperture of cages before using them on real nests. For clutches without exclusion cages, egg predators which were detected were Swamp Harrier *Circus approximans* (30.3%), Little Raven (24.2%), a rat (Muridae) (3.0%), and a Buff-banded Rail (3.0%). Cameras failed to identify predators in 12.0% of clutch losses.

The predator assemblage occurring in the immediate vicinity of predator exclusion cages significantly differed from that at nests without cages (one-way ANOSIM, Global $R = 0.144$, $P = 0.009$). SIMPER analysis attributed this dissimilarity to the contributions of Little Ravens (42.4%) and Swamp Harriers (37.0%). Little Ravens were the primary predator attracted to nests with exclusion cages whereas Swamp Harriers were attracted only to nests without cages. However, there was no significant difference in the number of potential predator visits, determined by visible

Table 6. Case studies of simple survival analysis using camera data on ground-nesting bird clutches. The results show a comparison of survival between rural and urban habitats (with rural nests as the reference variable).

Species	Factor	Model estimate (\pm se)	Z value	P	R ²	Sample size	df
Masked Lapwing (Mackay)	Habitat	2.274 \pm 1.79	1.27	0.204	0.20	23	20
	Estimated days to hatching	0.182 \pm 0.09	1.82	0.068			
Masked Lapwing (Phillip Island)	Habitat	1.740 \pm 1.28	1.36	0.174	0.40	32	29
	Estimated days to hatching	-0.193 \pm 0.08	-2.59	0.010			
Bush Stone-curlew	Habitat	18.34 \pm 7171.26	<0.01	0.998	0.06	16	13
	Estimated days to hatching	-0.06 \pm 0.16	-0.39	0.694			

Table 7. Case studies of days until fate by cover/caging at artificial nests mimicking Red-capped Plover nests.

Species	Model estimate (\pm se)	Z value	P	R ²	Sample size	df
Non-covered/ covered	1.669 \pm 1.332	1.253	0.220	0.048	33	31
Non-caged/ caged	-3.937 \pm 1.710	-2.303	0.026	0.101	49	47

identification of nearby predatory species on the ground by cameras, at the artificial nests fitted with exclusion cages (4.35 ± 0.60 visits) and the artificial nests without cages (4.24 ± 0.83 visits) ($t_{32} = 0.214$, $P = 0.910$).

Case study 4: real versus artificial nests

One project enabled us to examine whether different predator assemblages (i.e. the predators consuming eggs) were evident in different experimental treatments, which may occur if predators detect and are attracted to particular experimental conditions. An ANOSIM based on a zero-inflated Bray-Curtis dissimilarity matrix revealed a significant difference in predator assemblages (from presence/absence data). First, the predator assemblage consuming artificial clutches on coasts differed from the assemblage of egg predators which preyed on real Hooded Plover eggs (one-way ANOSIM, Global $R = 0.111$, $P = 0.007$). SIMPER analysis revealed that corvids (39.4%; more common at artificial nests), Red Foxes *Vulpes vulpes* (17.9%; more common at real nests), Australian Magpies *Gymnorhina tibicen* (10.3%; more common at real nests) and rodents (9.8%; more common at artificial nests) contributed most to this dissimilarity. Corvids were primary predators of artificial clutches whereas a more diverse array of predators preyed on real clutches at notable rates; corvids and foxes consumed most real clutches (31.0% and 34.5% of depredated clutches, respectively), with Australian Magpies also consuming a substantial number of clutches (20.7%). We refrain from conducting a survival analysis of real versus artificial nests with our data set because of the lack of comparability in exposure between the nest types, that is, fixed for artificial nests but age-dependent for real nests.

Discussion

Cameras used in our studies have revealed a broad array of shorebird egg predators, and wide variation in clutch success between populations of shorebirds in Australia.

Insights from the case studies

Cameras provided information on survival which, theoretically, could have alternatively been generated using periodic nest checks (Mayfield 1975). We revealed no differences in shorebird clutch survival between urban and rural habitats; despite our prediction, this result is unsurprising given the wide variation in reported trends in the available literature (Vincze *et al.* 2017). Here, the lack of difference may result from the fact that we studied species which were evidently well able to survive in urban habitats, being relatively large and/or aggressive (Cardilini *et al.* 2013). We note that urban and rural habitats may vary in many ways which could influence hatching success, and that we did not directly measure these covariates. While nest cover did not appear to vary between urban and rural habitats (M.A. Weston pers. obs.; and lapwings exclusively nested in open areas), predator assemblage and other prevailing threats may have been similar or varied with urban versus rural habitats (Cardilini *et al.* 2013). Simple comparisons between habitats can fail to reveal the complex mechanisms which drive habitat-specific reproductive success (Baudains & Lloyd 2007).

Using artificial nests, we found no difference in success of covered versus open nests, perhaps because predation was dominated by corvids regardless of the microhabitat, and reptilian or rodent predators, groups associated with cover, were generally absent or very rare, respectively. The small scales over which our comparisons occurred, coupled with the high mobility of the egg predators identified by the cameras, suggests that selective pressures other than predation may be involved in microhabitat and nest placement decisions. These may involve selection of suitable thermal or stress environments (Tan *et al.* 2015). We note that small sample sizes may have been associated with low

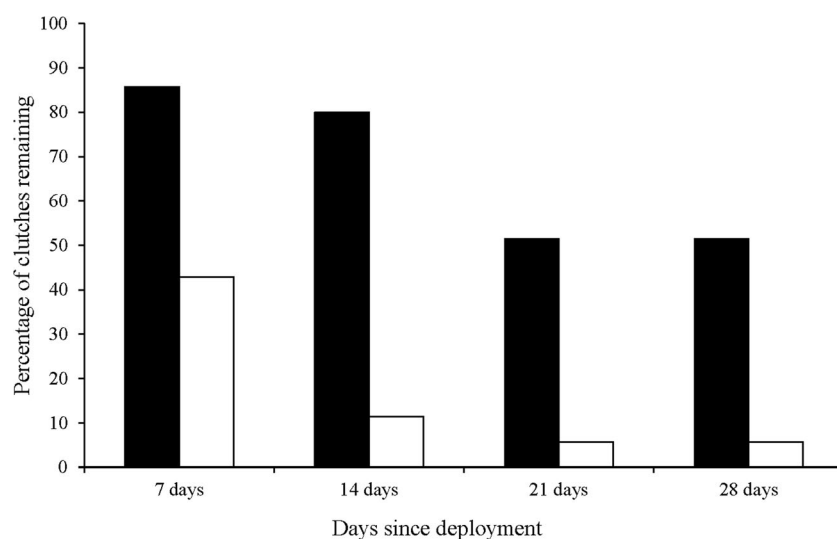


Figure 5. Percentage survival of artificial clutches in ($n = 35$) and outside ($n = 35$) predator exclusion cages, at 7, 14, 21 and 28 days after deployment, as assessed by regular checks and cameras. Black bars indicate nests with exclusion cages, open bars indicate controls.

statistical power in these comparisons, and as such, further studies with more replication are required to confirm these findings.

Predator exclosures increased clutch survival substantially (Tan *et al.* 2015) but this study identified that exclosures attracted a specific assemblage of potential predators. Such predators may attack incubating adults or chicks leaving the cage, and some of our images show Little Ravens taking Red-capped Plover chicks as they leave exclosures, providing further insight into the potential costs and benefits of this management technique.

Although regular checks can estimate survival, they provide only fragmentary and biased (e.g. diurnal, obvious fates) information on fate. While we had to use inference to assign fate to many nests, cameras generally provided better information on fate than previously available. We detected a different predator assemblage at real versus artificial nests on coastlines, suggesting that artificial clutches do not necessarily reflect loss of real clutches, a common criticism of artificial nest studies (Major & Kendal 1996) and a finding which has been reported for other breeding shorebirds (MacDonald & Bolton 2008). Most comparisons between artificial and real clutches measure survival, not fate (Mezquida & Marone 2003). Even when survival rates are the same, or correlated, between artificial and real clutches, the predators involved could differ (Guyn & Clark 1997). The use of artificial nests adds another level of complexity in that artificial nests are not an identical representation of real nests. We acknowledge the sampling frames of artificial and real nests were different, although they were broadly comparable. The visual cue of an

incubating adult either sitting on the nest or fleeing from it, and any olfactory and auditory cues associated with an incubating adult are absent from artificial nests; if present they might have helped predators locate nests more effectively (Ekanayake *et al.* 2015b). Predators such as corvids sometimes fly low in an attempt to flush incubating plovers from nests and then to search for eggs by walking from one nest site to the other (Persons & Applegate 1995). This study demonstrated that on sandy shores, real and artificial clutches (both with cameras) attracted different predator assemblages (see also DeGregorio *et al.* 2016), perhaps because of subtle differences in the selection of nest sites (artificial, by a human; real, by a plover), and/or because of the cues associated with incubating adult plovers. However, the fact that artificial nests do not reflect the exact properties of real nests can be useful. Experiments monitoring artificial nests help demonstrate the merits of particular management options, such as predator exclusion cages, and indicate that different predator assemblages are attracted to managed versus unmanaged nests and also to artificial versus real nests. In the case of exclosures, the enhanced survival of clutches described here is borne out in real plover nests (Tan *et al.* 2015).

Limitations of using trail cameras

Our cameras enabled the evaluation of success rates of shorebird nests, often confirming rather than inferring survival to hatching. That is, actual images of chicks were obtained with cameras, as opposed to the discovery of an empty nest around the probable hatching time during regular nest checks. For

threatened species such as the Hooded Plover, the distinction is particularly important, as observers have had a tendency to record failure at the egg stage when chicks are not observed, however camera data suggest that under such circumstances, chicks have often hatched but not survived long thereafter (G. S. Maguire 2016, unpubl. data).

One caution of using cameras to evaluate clutch success is that the same issues regarding 'exposure' hold as they do for other methods of quantifying success rates. Specifically, clutches discovered later in incubation have already survived longer so have improved probabilities of surviving to hatching compared with clutches discovered earlier. We addressed this by ageing clutches, using known incubation durations, and factoring a measure of 'exposure' (i.e. days to hatching) into our models. The significant effect of age is unsurprising, but the absence of a significant effect (reported here for several species) may result from low power associated with the age term in the models, or a non-random sampling of nests with respect to their vulnerability, that is, more vulnerable nests may have entered the study at higher ages.

The presence of a camera may attract or repel predators and incite a behavioural response from the predator such that fate and survival is not as it would be in the absence of a camera (Meek *et al.* 2016). Indeed, the time to clutch depredation decreases with increasing numbers of camera deployments in at least one study, involving high-density deployments of cameras and high corvid densities (Ekanayake *et al.* 2015c). Alternatively, some animals can display behavioural responses such as camera avoidance which is reflected by significant decreases in predator detection rates over time (Wegge *et al.* 2004). Camera avoidance has also been attributed to social status and territory boundaries of some animals, to neophobia, and/or to wariness towards objects or locations associated with human presence (Cutler & Swann 1999, Séquin *et al.* 2003). Although more studies are required, for our study species, cameras do not apparently affect hatching probability for at least Masked Lapwings (Cardilini *et al.* 2013).

The number of cameras available can limit the ability to monitor nests, potentially decreasing the statistical power of comparisons of clutch survival or compromising nest crypsis to the extent that subtle variation in success and fate are undetectable. Indeed, while our camera studies reported no difference between urban and rural Masked Lapwing clutch success on Phillip Island, a larger sample involving nests with and without cameras revealed a significant difference (Cardilini *et al.* 2013). Similarly, artificial

Red-capped Plover nests without cameras revealed that covered nests had higher survival (Lomas *et al.* 2014, Ekanayake *et al.* 2015c) while our camera-only sample revealed no such difference. A prudent approach may therefore be to monitor nests with and without cameras, to increase replication and enable detection of an effect of camera presence.

The cameras in this study revealed fates which would otherwise not have been detectable, but the occurrence of a reasonable proportion of nests for which fate could not be assigned means the *possibility* of bias exists. For example, small or fast egg predators may have been under-represented or absent simply because they were not detected (Hernandez *et al.* 1997, Cutler & Swann 1999). In our studies, possible predators, such as rats, could have gone undetected and contributed to fates classified as unknown. A bias can also exist due to factors relating to predator foraging behaviour, competition among predators, seasonality and also due to factors relating to camera location characteristics such as degree of human activity and type of habitat (Larrucea *et al.* 2007, Harmsen *et al.* 2010, Grendelmeier 2011). We studied shorebird species across a spectrum of body sizes, and the lack of difference in the degree of inference of nest fates suggests cameras may be equally useful for many different species. Furthermore, trail cameras can be prone to mechanical and battery failures, software glitches producing incorrect time stamps and irretrievable images, and to programming errors by researchers themselves (Rice *et al.* 1995, Hernandez *et al.* 1997). Such sources of potential error were not evaluated in our studies. Cameras can also be stolen, and while we experienced this, it occurred at low rates even in especially busy areas. In their review of the use of cameras to examine fate in European shorebirds, MacDonald & Bolton (2008) regard cameras as enabling the least-biased method available. Here, we acknowledge that any of the limitations described above may apply to our data; all available methods are imperfect.

Benefits of using trail cameras

Among the benefits of camera studies such as these is the incontrovertible evidence which is collected of some controversial egg predators (e.g. domestic dogs) and we note that images are especially influential when consulting land managers about issues affecting clutch success (G.S. Maguire 2016, pers. obs.). Cameras can also be useful in gathering evidence of the impact of introduced predators (e.g. feral cats *Felis catus*) and for investigating the efficacy of control methods (Brook

et al. 2012). In some cases, our photographic evidence has helped reveal that emergent native predators may have a greater impact than previously assumed, sometimes a greater impact than some introduced predators. We note the predominance of corvids as predators of shorebird eggs (see also Ekanayake *et al.* 2015c, Rees *et al.* 2015) and this study adds to the growing evidence that corvids are major egg predators in many Australian ecosystems. Cameras can also assist with answering key questions regarding 'controversial' management techniques, such as the use of predator exclusion cages (Tan *et al.* 2015). Predator exclusion cages on nests attract a different assemblage of predators, confirming the suspicion (and concern) that cages compromise the crypsis regarding nest locations, however cages still conferred benefits in terms of enhanced clutch survival. Cages may attract neophilic opportunistic species which may then learn an association between cages and clutches (Bytheway *et al.* 2016).

Cameras can also capture incidental but useful information regarding behaviour and ecology. Parental nest defence, care and escape behaviours were captured, and some engraved leg flags could be read from images. These observations would be unlikely during traditional nest visits because of disruption to normal behaviour at and around the nest. They represent a peripheral benefit to the use of cameras.

Another widely known benefit is the efficiency and non-invasiveness of using trail cameras (Silveira *et al.* 2003). As for all our case studies, the collection of the large amount of data at the nest would not have been possible without the use of trail cameras (Lusk *et al.* 2006, Demers & Robinson-Nilsen 2012, DeGregorio *et al.* 2016). Also for the majority of cases, the lack of an effect of camera presence on the probability of clutch depredation provides further evidence for the non-invasiveness of the use of trail cameras in nest fate studies (Cardilini *et al.* 2013, Ekanayake *et al.* 2015a).

Conclusion

By way of case studies, we present only a few of the many potential applications of trail cameras aimed at understanding clutch success and fate in shorebirds but suggest that we have demonstrated cameras can be an efficient, relatively non-invasive tool for data collection. We acknowledge that until studies are available which correlate metrics of success derived from camera and traditional methods, across an array of taxa and nesting contexts, cameras should be regarded as providing an index of success rather than an absolute estimate. While cameras remain the only tractable way to determine fate, inference is often required when

assigning fates and the failure to document all causes of fate means the possibility of bias exists. When they are used across factor levels in any given study, any reported differences between levels would generally seem to be reliable. Moreover, they have elucidated a range of hitherto unrecognized clutch fates, and provide compelling and influential evidence for fate in the form of images. The incorporation of camera-derived nest success data into spatially modelled land management scenarios (Laidlaw *et al.* 2017) offers a promising approach to help manage the viability of populations of breeding shorebirds.

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