

Tracking day and night provides insights into the relative importance of different wader chick predators

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Poor reproductive success driven by nest and chick predation severely limits the population recovery of waders breeding on lowland wet grassland. Managing predation requires knowledge of the predators and because these can be grouped into nocturnal or diurnal hunters, detecting the timing of predation can help assess their relative impacts. Wader nest studies investigating the timing of egg predation have identified nocturnal mammals, primarily Red Foxes *Vulpes vulpes*, as the most important nest predators, but quantifying predator importance for highly mobile wader chicks is more difficult. Manual radiotelemetry can detect whether chicks are alive but cannot detect the time of predation, and predator identity can be determined only in the few cases where remains are recovered. As an alternative we used automatic radio tracking stations (ARTS) to constantly record the signals and predation timing of 179 radiotagged Lapwing *Vanellus vanellus* chicks, combining this with manual telemetry, inference about predator identity from predated remains and site-level Fox, mustelid and avian predator activity monitoring. This approach succeeded in detecting the time of predation for 60% of the 155 chicks that were predated. Diurnal chick predation accounted for a larger number of predation events, but nocturnal predation was more intensive in terms of predation likelihood per hour. Mammalian predation during both day and night had a larger impact on chick survival than did avian predation. Raptors were primarily responsible for predation by birds and Foxes for predation by mammals, with Foxes also having a larger influence on daily chick predation rates than other predators. Chick predation increased seasonally, implying that earlier-hatching breeding attempts are more likely to be successful. Higher Fox, raptor and mustelid activity resulted in higher proportions of chicks being predated by those predators, so quantifying the activity of those three predator groups on a site could be a quicker alternative to studying chicks when investigating which predator species to target with site-specific predation management.

Keywords: automatic radio tracking stations, Common Redshank *Tringa totanus*, Fox, lowland wet grassland, mustelid, Northern Lapwing *Vanellus vanellus*, raptor, timing of predation.

Populations of farmland birds once common across Western Europe have declined dramatically in recent decades as a result of agricultural intensification and land-use change (Donald *et al.* 2001, BirdLife International 2004). Wader species breeding on lowland wet grassland are of particular concern (Thorup 2006), suffering range contractions

that now restrict declining populations to isolated protected sites (Wilson *et al.* 2005, Balmer *et al.* 2013). On these sites, predation of both nests and chicks limits breeding success, contributing to ongoing declines and preventing population recovery (Peach *et al.* 1994, Langgemach & Bellebaum 2005, MacDonald & Bolton 2008, Teunissen *et al.* 2008, Schekkerman *et al.* 2009, Roodbergen *et al.* 2012). Determining the predators involved and managing their impacts (e.g. through exclusion,

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habitat manipulation to reduce impacts, diversionary feeding or lethal control; Bolton *et al.* 2007, Malpas *et al.* 2013, Laidlaw *et al.* 2015) is now a key management necessity.

Predator–prey systems are dynamic and involve multiple interactions between different predator species as well as between predator and prey (Holt 2002, Laidlaw *et al.* 2013). Monitoring the predators as well as the prey in any system in which the survival of the prey species is of interest is therefore an important consideration (MacDonald & Bolton 2008). The predators operating on lowland wet grassland can be characterized by their period of activity; detecting the timing of predation can thus indicate the predator type involved. Nocturnally active predators on wet grassland are usually mammalian (Red Fox *Vulpes vulpes*, European Badger *Meles meles*, European Hedgehog *Erinaceus europaeus* and small mustelids: Stoat *Mustela erminea*, Weasel *Mustela nivalis*, American Mink *Neovision vison*), except in rare circumstances where owls are also present (Barn Owl *Tyto alba*, Long-eared Owl *Asio otus*, Short-eared Owl *Asio flammeus*). Diurnally active predators are primarily avian (raptors, gulls, corvids and herons), although mammalian predators can also be active during the day. Studying the timing of wader nest predation using temperature data-loggers and nest cameras has implicated nocturnal mammals, particularly Foxes, as primarily responsible for wader nest mortality (Teunissen *et al.* 2008, Eglington *et al.* 2009). However, breeding success remains low despite management aimed at reducing nest predation (Bolton *et al.* 2007, Malpas *et al.* 2013), suggesting that chick survival may be the more important demographic parameter (Sharpe *et al.* 2008).

In contrast to nest predation, recent studies indicate that diurnally active avian predators are chiefly responsible for wader chick mortality (Junker *et al.* 2004, 2006, Schoppenhorst 2004, Hönisch *et al.* 2008, Teunissen *et al.* 2008, Schekkerman *et al.* 2009). However, the results of these tracking studies, in which predator types were inferred from chick remains recovered through manual telemetry, are not supported by those of mammalian predator removal and exclusion trials, in which wader nest survival, chick survival and fledging success increased, after nocturnal predation pressure from mammals (Foxes and Badgers) was reduced (Bolton *et al.* 2007, Schifferli *et al.* 2009, Rickenbach *et al.*

2011, Malpas *et al.* 2013). A possible explanation for these different results is that the likelihood of finding prey remains is dependent on the cause of mortality (Schaub 2009) as well as the search intensity, potentially biasing tracking studies towards bird-predated remains, which may be easier to find (e.g., plucked close to the predation site or high up in a nest or plucking post where there are no impediments to tag signals). Mammalian predators, on the other hand, may be more likely to cache remains in thick vegetation or underground and damage tags through chewing or digestion, making them harder to relocate.

A way to remove this potential source of bias is to monitor the timing of chick predation to compare the relative importance of diurnally active avian and nocturnally active mammalian predators. This has been attempted using dawn and dusk manual telemetry surveys to classify predation as nocturnal or diurnal (Rickenbach *et al.* 2011), but such surveys are time-consuming and may result in the misclassification of very early or late predation events. As an alternative, we suggest that automatic radio tracking stations (ARTS), which constantly search for and record signals from radiotags, could be used to determine the timing of predation more accurately. ARTS are a relatively new technology now increasingly used to monitor temporal and spatial movements of birds, mammals and fish in foraging, migration and behavioural studies (e.g. Green *et al.* 2002, Briner *et al.* 2003, Kays *et al.* 2011, Thorstad *et al.* 2013).

In this study, we combine the use of ARTS, manual chick tracking and predator monitoring methods as well as conventional inference based on predated remains to provide insights into the relative importance of different wader chick predators in limiting Northern Lapwing *Vanellus vanellus* chick survival on lowland wet grassland.

METHODS

Study sites

We monitored 15 UK lowland wet grassland sites chosen to represent the geographical ranges of lowland wet grassland and breeding waders in the UK and expected to have ≥ 10 breeding wader pairs at varying nesting densities (Fig. 1, Table 1; Jefferson & Grice 1998, Balmer *et al.* 2013). Some sites were monitored in multiple years

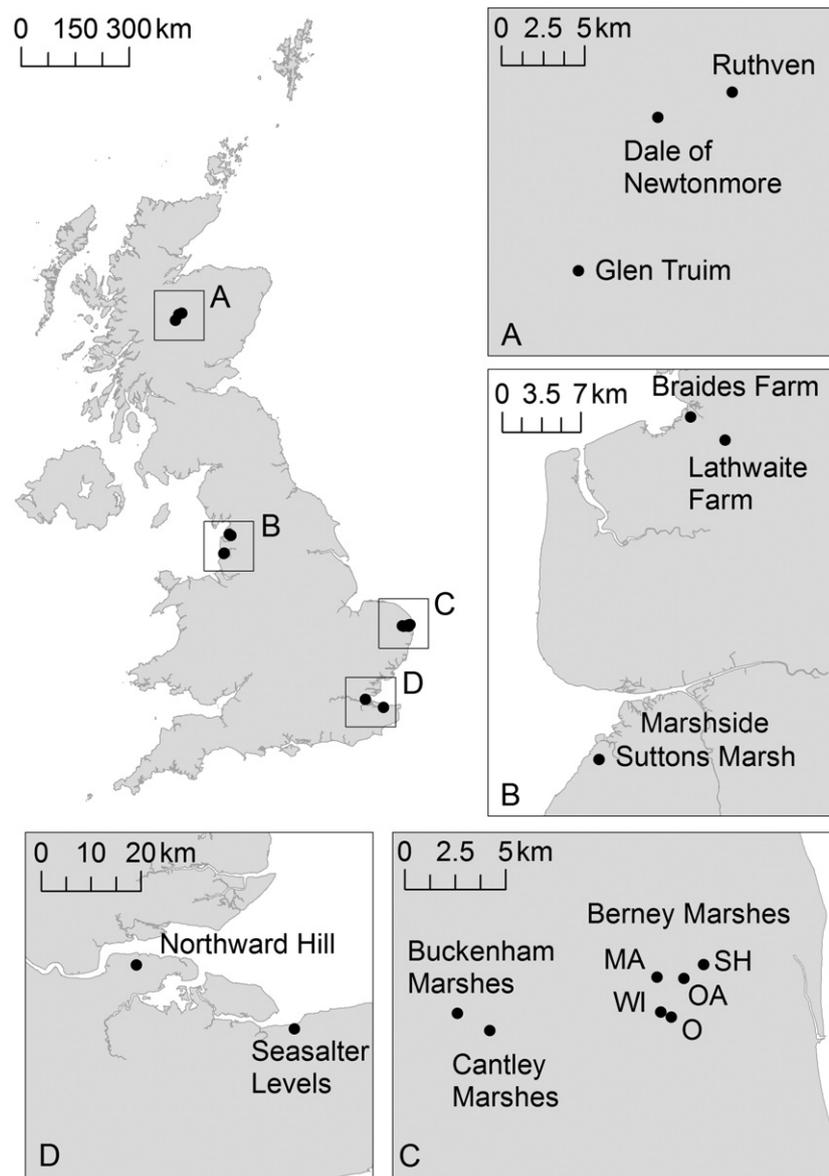


Figure 1. Map showing the location of study sites. Insets (A–D) show locations of clustered sites; Berney Marshes sites in C are Machete (MA), Office (O), Old Arable (OA), Shearman's (SH) and Wickhampton (WI). Note that scales vary.

(2009–2013) and because site-specific predation effects were expected to vary annually, we categorized these as independent 'site-years' for analysis (18 site-years, Table 1). All sites were nature reserves or protected areas managed for their breeding wader populations through agri-environment schemes or targeted advisory input from conservation organizations (Smart *et al.* 2006, Eglington *et al.* 2010). Sites comprised multiple fields bounded by wet ditches and accessed by gateways/crossings. No mowing or machinery

operations took place during the wader breeding season but lethal control of Foxes (shooting at night by trained marksmen) and Carrion Crows *Corvus corone* (e.g. Larsen cage traps) was conducted on or around most sites before (Foxes) and during (Crows) the wader breeding season following legal welfare requirements (Table 1). Predator management of this kind is now common practice on and around sites managed for breeding waders (Bolton *et al.* 2007). This study therefore represents the levels of chick survival and predator

Table 1. Site-years in which Lapwing chick survival and predator activity was monitored (F, Fox; A, avian; M, mustelid; –, no monitoring).

Site	Year	No. of chicks tagged	Monitoring area (ha)	Lapwing breeding density (nests/km ²)	Predator monitoring	Lethal control ^a
Berney Marshes: Machete	2009	5	29	62.1	– A –	F & C (on & S)
Berney Marshes: Office	2009	11	49	61.2	– A –	F & C (on & S)
Berney Marshes: Old Arable	2009	10	54	64.8	F A M	F & C (on & S)
Berney Marshes: Shearman's	2009	16	60	66.7	F A M	F & C (on & S)
Berney Marshes: Wickhampton	2009	9	43	88.4	F A M	F & C (on & S)
Berney Marshes: Old Arable	2010	1	54	75.9	F – M	F & C (on & S)
Berney Marshes: Shearman's	2010	24	60	78.3	F A M	F & C (on & S)
Berney Marshes: Wickhampton	2010	11	43	172.1	F A M	F & C (on & S)
Buckenham Marshes	2010	10	40	60.0	F A M	F & C (on & S)
Marshside: Suttons Marsh	2011	9	68	19.1	– A M	F* (S)
Cantley Marshes	2012	17	48	41.7	F A M	F & C (on & S)
Northward Hill	2012	14	18	116.7	F A M	F & C (on)
Seasalter Levels	2012	3	27	33.3	F A M	F & C (on)
Braides Farm	2013	6	13	130.8	F A M	F (S)
Dale of Newtonmore	2013	9	19	57.9	F A M	F* & C* (S)
Glen Truim	2013	8	39	17.9	F A M	F* & C* (S)
Lathwaite Farm	2013	4	8	112.5	F A M	F (S)
Ruthven	2013	12	44	22.7	F A M	F* & C* (S)

^aLethal predator control: F = Fox; C = Carrion Crow; on = lethal control conducted on chick monitoring site if necessary to control predation in breeding season; S = control conducted on land immediately adjacent to site; * = control likely but not confirmed.

activity characterizing typical lowland wet grasslands managed for breeding waders in the UK.

Wader chick monitoring

The relatively abundant and easy-to-monitor Northern Lapwing was chosen as a study species. Lapwings often nest in close proximity to other wader species (e.g. Common Redshank *Tringa totanus*, Black-tailed Godwit *Limosa limosa*), and although their nesting ecology and adult predator defence behaviours differ (Cramp & Simmons 1983, Kis *et al.* 2000), their nests are subject to similar predation rates (MacDonald & Bolton 2008). We also expected Lapwing chicks to be subject to similar predation pressures to those of other wader species, as they congregate around the same wet features (Beintema *et al.* 1991, Smart *et al.* 2006, Eglington *et al.* 2010) and have similar responses to predators (crouching when young, running when older; Walters 1990).

In all, 179 Lapwing chicks (Table 1) were ringed and fitted with unique combinations of permanent colour rings or temporary leg flags and a 0.4–0.5 g radio tag 10–15 mm in length with a 12–15 cm hair-thin whip antenna (2009–2010: Biotrack, Wareham, UK; Holohil Systems, Ontario,

Canada. 2010–2013: Perdix Wildlife Supplies, Kenilworth, UK). Tags were mounted on gauze with Araldite or Superglue adhesive and attached to the down feathers over the pelvic girdle using water-based latex adhesive (Copydex). Down feathers were folded over the gauze and tag on adhesion to reduce visibility. This method has commonly been used in similar chick predation studies with no reported negative effects (Hönisch *et al.* 2008, Teunissen *et al.* 2008, Schekkerman *et al.* 2009). Tags pulsed at individual frequencies of 173.001–173.999 MHz with an average beeps rate of 33 beeps per minute (BPM).

Chicks were manually tracked and captured to re-glue tags if necessary every 8 days (the minimum recommended by Sharpe *et al.* 2009 to prevent recapture-related mortality) using Telonics TR4 or ATS R2000 receivers and handheld Yagi antennas (receivers: Telonics, Mesa, AZ, USA and Advanced Telemetry Systems, Isanti, MN, USA; antennas: Biotrack). Brood size and location observations were made from a suitable distance to minimize disturbance. Tags had an expected battery life of 30 days, similar to the fledging period for Lapwing (35–40 days; Cramp & Simmons 1983) and were removed just before this battery end date if predation did not occur and if the chick

could be recaptured. The majority of chicks were ringed and tagged on hatching (164/179). This sometimes resulted in a tag life shorter than the duration of the fledging period, so part-grown chicks from broods of unknown hatch date (15/179) were also tagged to account for any age-dependence in survival from hatching to fledging (Bolton *et al.* 2007). The age of part-grown chicks (days) was estimated using site-year specific regression equations of age on bill length (mm) from recaptured chicks of known age, or using published equations where site-year data from this study were limited (Mason & Smart 2015). In some cases, up to three chicks per brood were tagged to increase the sample size of chicks for analysis (one-chick broods, $n = 79$; two-chick broods, $n = 47$; three-chick broods $n = 2$).

Tracking day and night

Each ARTS was a multi-directional antenna mounted on a 4 m pole and connected to a logging receiver and 12 V battery (Receiver: DataSika B; Biotrack. Antenna: Base Station

Antenna BS3; RW Badland, Stourbridge, UK). Up to two ARTS per site-year were either placed near the centre of areas where tagged wader broods congregated or set to target individual broods, and could detect tag signals optimally within a 250 m radius (Figs 2 and S1). ARTS scanned for up to 20 tag frequencies on a cyclical 24 h basis, scanning each frequency for 30 s and recording the date, time to nearest second, BPM and relative signal strength from each tag pulse detected. Tag signal strength and therefore ARTS detection rate were lowest when chicks were being brooded, hiding or dead (adults or vegetation impeding tag signals) and strongest when chicks were active and moving. Daily fluctuations in tag signal strength were recorded for some Lapwing chicks (signal peaking at night); these could hypothetically result from temperature-induced tag frequency drift, diel patterns of chick activity or a reduction in ambient noise interference at night (see Appendix S1 for a discussion of these effects). These fluctuations did not affect the detection of mortality events, which always manifested as

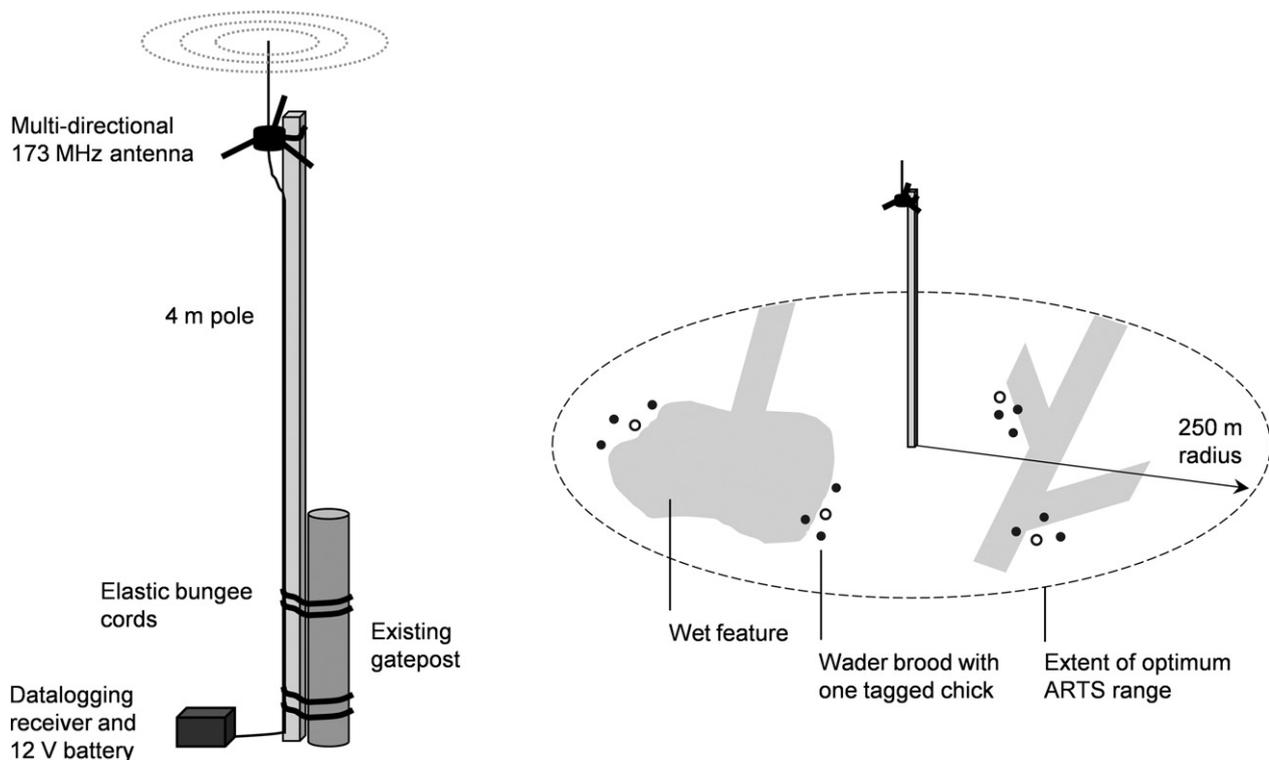


Figure 2. Diagrammatic representation of a typical automatic radio tracking station (ARTS) set up to follow a congregation of wader broods on lowland wet grassland wader breeding fields.

signal disappearances or suspicious changes in the usual fluctuation pattern.

Data were exported from the receiver to a laptop computer every 2–3 days using the DATASIKA HOST Application (Biotrack, 2009) and visually examined in Microsoft EXCEL (2007) for any suspicious changes in tag output that might indicate a mortality event (usually the sudden disappearance of a tag signal or an unexpected reduction or increase in signal strength out-with daily signal fluctuations; Appendix S1). Any suspicious ARTS data changes were then investigated using manual telemetry, surveying in ever-widening circles from locations in which chicks were last observed up to a distance of 2 km. Chicks were recorded as predated if ARTS data indicated a distinct change in tag signal followed by the recovery of predated remains, or if the tag signal and chick disappeared before the expected date of tag battery failure/fledging and its parents were no longer chick calling or alarming. Chicks found dead with no visible signs of trauma (easy to find with manual telemetry as tags were undamaged and remains were in the last-known brood location) were recorded as dying of causes other than predation based on visual observations (starvation, exposure or drowning; Teunissen *et al.* 2008) irrespective of ARTS evidence. Tag failure was assumed when tag signals disappeared but the tagged chick was still observed alive in the expected brood location (in these cases, chick fate was classed as unknown). Chicks were considered to have survived the 30 day monitoring period if tags were removed from well-feathered chicks (Bolton *et al.* 2011) at the end of tag battery life or if chicks were observed to have fledged before tags could be removed. If signal changes resulted from tagged chicks moving out of ARTS range, ARTS stations were moved to ensure all broods were adequately covered (this did not influence predation detection from ARTS data).

On confirmation of chick predation, ARTS data were examined to identify the exact time at which the tag signal disappeared or changed suspiciously as above, accurate from 2 s to 10 min depending on the number of programmed tag frequencies. Detection of predation timing in this way was clear and reliable (Appendix S1) unless ARTS data were intermittent due to chicks moving out of range before predation, in which case predation time was classed as unknown. Predation events were attributed to day or night based on how

timings compared to morning and evening UK Civil Twilight (CT): diurnal predation events occurred between morning and evening CT; nocturnal events between evening CT and morning CT the following day.

Identifying predators from timing of predation and remains

Predator types were inferred from both the timing of predation and the location and characteristics of remains following example criteria in Table 2 and Teunissen *et al.* (2008). All nocturnal predation was attributed to mammals, as these were the only nocturnal chick predators present on our sites. Only one nocturnal avian predator was ever observed (Barn Owl, 2 site-years only) and there was no evidence of it being perceived as a threat by waders, or of it predated chicks (Table S1). Both mammalian and avian predators were active on our study sites during the day, so diurnal predation was attributed to predator species based on inference from recovered remains. Inferring predator type from predation timing in this way is a common method used in wader nest survival studies (Teunissen *et al.* 2008, Eglington *et al.* 2009).

Inference regarding the importance of individual predator species was based on characteristics of remains compared with the outcomes and characteristics of observed predation events (Table 2). Full written histories of chick fates, timing of predation and remain characteristics were additionally examined by one person at the end of the project to ensure consistency in predator inference between site-years.

Predator monitoring

We used rapid assessment methods to monitor the activity of three predator groups known to predate lowland wader nests and chicks (Junker *et al.* 2004, Schoppenhorst 2004, Hönisch *et al.* 2008, Teunissen *et al.* 2008, Schekkerman *et al.* 2009, Rickenbach *et al.* 2011) during the same period as chicks were monitored in each site-year (Table 1).

To assess Fox activity, faecal (scat) transects were conducted at the beginning (April–late May) and end (May–June) of the wader chick monitoring period in each site-year when wader chicks were most active (Webbon *et al.* 2004). Transects

Table 2. Examples of the location and characteristics of recovered predated radiotagged chick remains used to infer the identity of chick predators. Also see Teunissen *et al.* (2008).

Predator	Timing, location and state of remains
Unknown	ARTS data and chick disappearance suggest predation but timing of predation not clear, remains not recovered or characteristics of remains not specific enough to suggest predator species
Avian	
Unknown avian	Daytime predation and remains characteristic of avian predator (e.g. tag plucked not bitten) but not specific enough to suggest species
Unknown raptor	Tag with plucked feathers torn out not bitten; tag found plucked a long way (> 500 m) from where chick last seen (>500 m), antenna bent sharply by bill
Marsh Harrier <i>Circus aeruginosus</i>	Predation event observed; remains suggest raptor predation (above) and spp. observed hunting in vicinity of chick 5 mins either side predation time
Common Buzzard <i>Buteo buteo</i>	Tag found in or underneath nest; remains suggest raptor predation and spp. observed hunting in vicinity of chick at time of predation
Common Kestrel <i>Falco tinnunculus</i>	Tag found in nest; remains suggest raptor predation and spp. observed hunting in vicinity of chick at time of predation
Peregrine Falcon <i>F. peregrinus</i>	Tag at plucking site
Mammalian	
Unknown mammal	Nocturnal predation and/or remains characteristic of mammalian predator (chewed, bite marks, cached, limbs bitten off)
Unknown mustelid	Small bite marks to the back of neck or head; carcass cached in grass tussock
Red Fox <i>Vulpes vulpes</i>	Tag or ring in scat; tag in or around burrow; legs, rings and tag found chewed or bitten off next to fox scat; whole broods predated in quick succession
Weasel <i>Mustela nivalis</i>	Predation event observed; bite marks to back of head and carcass partially eaten leaving the skin, head and legs intact

followed linear features encompassing access routes and the inner circumference of chick monitoring fields. The first visit aimed to clear scat deposited the previous winter; the second recorded scats deposited by Foxes active during the monitoring period. Our measure of Fox activity was the relative Fox density (scat/km/day) based on the number of scat recorded on the second visit, the length of transect walked (km; MAPINFO PROFESSIONAL v6 2000) and the number of days since the first transect.

Mustelid activity was monitored using tracking tunnels. In 2009/2010 these consisted of wooden tunnels over a clay tracking cartridge built following the specifications of the Game and Wildlife Conservancy Trust mink raft (Reynolds *et al.* 2007). Mink raft tracking cartridges were modified for use on land by replacing baskets with 150 × 100 × 45 mm plastic food containers which could be filled with water and sunk level with the ground. In 2010–2013 this design was replaced by black corrugated plastic tunnels with a wooden base and ink and paper tracking cartridge as described in Laidlaw *et al.* (2013). This change in tunnel design was made to increase fieldwork efficiency (plastic tunnels were lighter, so were easier to store, transport and set up) rather than

concerns over wooden tunnel efficacy. In all site-years an average of 0.5 tunnels per hectare were placed around the circumference of chick monitoring fields in positions most likely to intercept mustelids (long vegetation, gateways, ditch crossing points). Tunnels were activated in the first week of chick monitoring in each site-year (late April–early May) and checked weekly for 3 weeks. On each visit the tracking medium was examined for the presence/absence of mustelid prints and the tracking cartridge refreshed. Mustelid activity (mustelid presence/tunnel/day) was calculated for each visit by dividing the number of tunnels with mustelid prints by the total number of tunnels on site, and then dividing this by the number of days since the tunnels were last checked. This was then averaged across the three tunnel visits to provide a mustelid activity estimate for the chick monitoring period for that site-year. Although we have no validation data to compare the two tunnel designs directly, anecdotally we encountered no differences in tunnel-use by mustelids nor in the ease with which mustelid prints could be identified between the two designs, and mustelid activity rates averaged across site-years using each method did not significantly differ (mean mustelid presence/tunnel/day wood = 0.003 ± 0.004 95% CI,

$n = 4$ site-years; plastic = 0.002 ± 0.001 , $n = 12$; $t = 0.79$, $P = 0.48$).

Avian species with the potential for chick predation are numerous in lowland wet grassland landscapes and could include many raptors, corvids, gulls, herons and egrets. As some may never predate wader chicks on a site-specific basis, automatically assuming predator effects would result in biased and meaningless estimates of predator activity. Rather than assume that all species actively preyed on waders in all site-years, we therefore used the predator deterrence behaviour of wader adults to inform our definition of a perceived avian predator in each site-year, considering that only species which waders perceived as a threat were likely to be actively involved in predation (Walters 1990). Lapwing adults actively deterred all raptor species present in all site-years but deterrence of other species (corvids, gulls, herons, egrets) was site-specific and dependent on individual predator behaviours (Table S1).

To estimate the activity of avian predators defined above during the period wader chicks were active, timed watches were conducted during the wader chick monitoring period in each site-year, from the date of first chick tagging to the date of final chick predation or fledging (mean start date 13 May, end date 11 June). In 2009 and 2011, watches were of varying frequency and duration (mean watch frequency per site-year = 10, range = 2–16; mean duration = 2.2 h, range = 1.4–2.9; mean total hours watched = 22 h, range 3–31) but in 2010, 2012 and 2013, watch length and frequency were standardized (minimum 2 h weekly) to allow time for other monitoring activities (mean frequency = 5, range = 2–10; mean duration = 2.2 h, range = 2.0–4.2; mean total hours watched = 11 h, range = 4–21). During timed watches in all site-years, all separate predatory passes by individual avian predators over the wader monitoring area were recorded, a pass defined as a potential predation event, i.e. any flight or strike exhibiting hunting behaviour (raptor species) or any flight, strike or foraging activity to which wader adults reacted with deterrence behaviour (corvids, gulls, herons, egrets). The total number of predatory passes/hour was calculated for each watch and averaged across all watches at a site to provide a site-year level estimate of avian predator activity, thus controlling for differences in watch frequency, watch duration and total number of watches (due to the

difference in chick monitoring period length) between site-years. The activity of all avian predators combined (all raptors, gulls, corvids, herons and egrets combined) and raptor activity were correlated (Pearson's $r = 0.39$, $t = 17.24$, $df = 1615$, $P < 0.0001$).

Drivers of chick survival

We used an extension of Mayfield logistic regression to investigate the effects of predator activity on daily chick predation probability (DPP; Aebischer 1999). This analysis method is still common in both chick and nest predation studies (Sharpe *et al.* 2009, Laidlaw *et al.* 2015, Dunn *et al.* 2016, MacDonald *et al.* 2016, Setchfield & Peach 2016) and is in this case preferable to other survival analysis methods (e.g. 'Survival-Time analysis', Nur *et al.* 2004) because it facilitates clearer interpretation of continuous covariate effects and better allows for the control of data non-independence where survival over time is not inherently of interest. We ran binomial generalized linear mixed models (GLMMs) in R (glmer, lme4: R Core Team 2013, Bates *et al.* 2014), with the daily predation outcome of each chick as a response variable (1 = predated, 0 = alive or dead for reasons other than predation) from the date of tagging to the date of predation, death, disappearance or tag removal up to 30 days after tag attachment. Models used a logit link, Laplace likelihood approximation and the random effects of chick identity nested within brood nested within site-year (to account for non-independence of chick-days from the same chick, multiple chicks from the same brood, and variation in predator abundance and chick survival between site-years). We were interested in testing the main effects of Fox activity, mustelid activity, all-avian predator activity and monitoring date (seasonal variation in survival; 1 April = day 1), and also included chick age (hatch day = age 0) as a control variable to account for any age-dependent effects on mortality (e.g. Bolton *et al.* 2007, Sharpe *et al.* 2009). Although two-way interactions between predator activity variables were biologically plausible, we only included main effects in our models, as including interactions would have resulted in model overspecification due to our relatively small dataset (full model parameters $n = 9$; binomial datapoints: success/predation $n = 133$, failure/survival $n = 1484$;

Harrell 2015). Variance inflation factors for variables were close to 1 in all cases (maximum = 1.14), indicating no multicollinearity. Model convergence was improved by first centring all variables (standardized $x = x - \text{mean}(x)/\text{sd}(x)$), and by using 'bobyqa' as the optimizer (Bates & Maechler 2009, Powell 2009). Only site-years with available Fox, avian and mustelid data were included (14 site-years, 153 chicks from 106 broods, Table 1). All assumptions of the Mayfield logistic regression method were fulfilled (Nur *et al.* 2004).

Model selection was based on AIC_c (Akaike information criterion with correction for small sample sizes), which selects the model best approximating the 'true' model (Burnham & Anderson 2002) but favours model complexity (Arnold 2010). We compared models with all possible combinations of covariate main effects, maintaining a constant random effect structure and conforming to marginality assumptions (dredge, MuMIn: Barton 2014). Top AIC_c models were selected as those with $\Delta AIC_c \leq 6$ that were not more complex versions of a model with a lower AIC_c (excluding models with uninformative parameters: Arnold 2010, Richards *et al.* 2011). Standardized regression coefficients (β ; Schielzeth 2010) for all covariates retained in top models were compared to determine relative effect sizes.

RESULTS

Of the 179 chicks tagged, 155 (87%) were predated, nine (5%) died from other causes (drowning, exposure) and 13 (7%) survived (Fig. 3). Only two chicks (1%) had unknown fates attributable to tag failure. These results represent very low survival rates, with a probability of chicks surviving predation beyond 30 days of monitoring across all site-years between 5.4% ($-2.0/+3.1\%$ 95% confidence interval (CI); Mayfield 1961) and 5.6% ($-2.5/+4.4\%$; Kaplan & Meier 1958) depending on the method used (see Table S2 for site-year specific estimates).

Timing of predation

The timing of predation could be determined for 93 (60%) of the 155 predated chicks (Fig. 4). A higher proportion were predated during the day (54 chicks: 58% of chicks where timing known, 35% of all predated) than at night (39: 42% of chicks where timing known, 25% of all predated). The number of chicks predated at night was, however, disproportional to the number of hours of darkness. Daylight was 7–12 h longer than darkness during April–July on our study sites (www.timeanddate.com; Fig. 4). Comparing the ratios of the proportion of chicks predated by

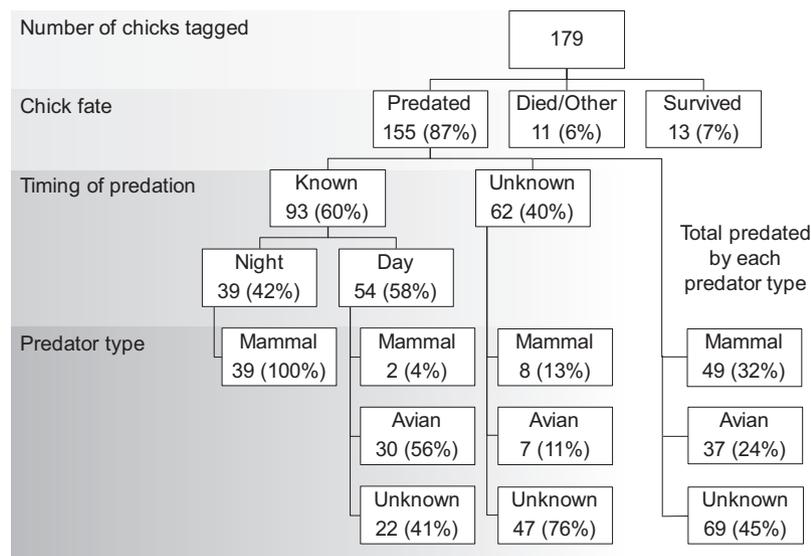


Figure 3. Summary of Lapwing chick survival results. From top to bottom, the diagram shows the proportions of radiotagged chicks that were predated, survived the 30-day monitoring period, or died or disappeared from other causes, followed by the timing of predation and the main predator types (inferred from timing of predation and predated remains). Boxes show the numbers of chicks in each category and this number as a percentage of the total one flow-level above it.

night (pN) or day (pD) with the proportion of hours of darkness (hN) or daylight (hD), nocturnal predation was 1.91 times more intensive than diurnal predation (nocturnal pN/hN = 1.53, diurnal pD/hD = 0.80).

Predator identification

Predated remains were recovered from 38% of chicks overall, although this varied between site-years (site-year mean = 42%; Table S3). Timing of predation information was available for 58% of those never recovered, although again this varied between site-years (mean = 61%). For all chicks where predator type could be determined, mammalian predation accounted for 10% more predation events than avian predation and was similar in terms of biological significance to diurnal predation (49 chicks predated by mammals, 54 predated diurnally; Fig. 3). All nocturnal predation was attributed to mammals (as mammals were the only nocturnal chick predators active on our sites), whereas both mammals and avian predators contributed to predation in daylight hours (Fig. 3, Tables 3 and S4). Where the timing of predation could not be determined, mammalian and avian predators were identified in almost equal proportions (Fig. 3), indicating that ARTS data were unbiased towards particular predation events (no over-representation of either predator

type in the undetected category). Foxes were the most frequently identified mammalian predator, active both night and day, and raptors were the most frequent avian predator. Foxes and raptors accounted for equal proportions of predation events (20%) and together contributed to 40% of predation mortality (Table 3).

It took longer to find mammal-predated (median time 4.5 days, range = 0–23 days) than avian-predated remains (median time 1 day, range = 0–9 days; Mann–Whitney $W = 158.5$, $P = 0.02$, 15 site-years). However, knowing the timing of predation did not significantly increase our ability to detect mammalian predation (59% of chicks predated by mammals where timing of predation was known, 52% where timing was unknown, $\chi^2_1 = 0.27$, $P = 0.61$, all site-years) nor were predated remains taken further away by avian predators (avian median distance from last chick location to predated remains = 194 m, range = 43–3702; mammalian median = 155 m, range = 0–1099; Mann–Whitney $W = 326.5$, $P = 0.277$, 14 site-years).

Drivers of chick survival

Monitoring date was the best predictor of DPP, being retained in all best fit models (Tables 4 and S5). The magnitude of the effect of date on DPP was relatively high (top model $\beta = 0.39 \pm 0.14$ se),

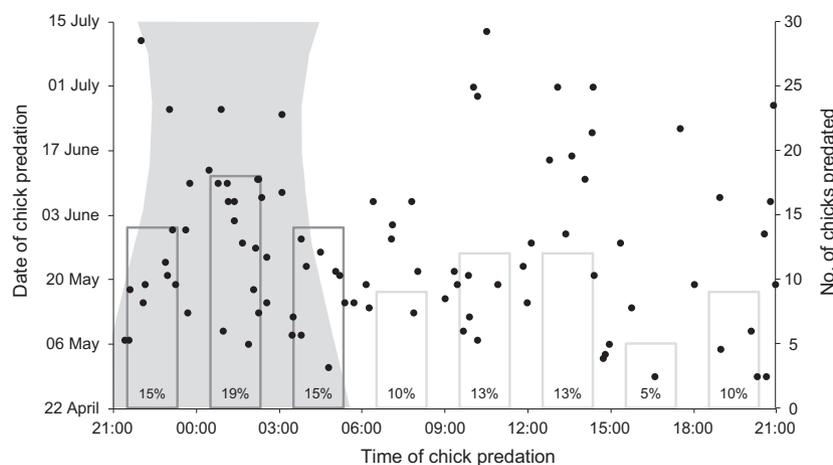


Figure 4. The timing of predation of Lapwing chicks. Columns indicate the numbers and percentage of chicks predated during 3-h time intervals (right-hand axis); points show the temporal distribution of predation events throughout the monitoring period (left-hand axis). Each point represents a predated chick ($n = 93$); overlapping points have been jittered by 20 min for clarity. Darker grey columns and grey shading indicate hours of darkness.

Table 3. Avian and mammalian predators identified as important in limiting Lapwing chick survival and the time at which predation occurred.

Inferred predator type	Timing of predation							
	Total		Day		Night		Unknown	
	Number	%	Number	%	Number	%	Number	%
Mammalian predator	58	37.4	7	4.5	39	25.2	12	7.7
Unknown mammal	16	10.3	0	0	14	9.0	2	1.3
Red Fox <i>Vulpes vulpes</i>	34	21.9	7	4.5	21	13.5	6	3.9
Mustelid (Weasel <i>Mustela nivalis</i> , unknown spp.)	8	5.2	0	0	4	2.6	4	2.6
Avian predator	43	27.7	32	20.6	0	0	11	7.1
Unknown bird	9	5.8	3	1.9			6	3.9
All Raptors	34	21.9	29	18.7			5	3.2
Unknown raptor spp.	21	13.5	18	11.6			3	1.9
Common Buzzard <i>Buteo buteo</i>	5	3.2	3	1.9			2	1.3
Common Kestrel <i>Falco tinnunculus</i>	5	3.2	5	3.2			0	0
Marsh Harrier <i>Circus aeruginosus</i>	1	0.6	1	0.6			0	0
Peregrine Falcon <i>F. peregrinus</i>	2	1.3	2	1.3			0	0

Shown are numbers of chicks predated and percentages of the total 155 chicks predated (Fig. 3). Avian and mammalian predators with the largest contribution to predation are shaded grey.

with chicks more likely to be predated each day as the monitoring period progressed (Fig. 5a), equating to a 30.2% probability of a chick surviving 30 days at the start of the season compared with a 0% probability at the end (22 April–13 July; 30 day fledging success = $[1 - \text{daily predation probability}]^{30}$; Mayfield 1961). Fox activity was also a good predictor of DPP, being retained in the top model with an effect magnitude of 0.31 ± 0.12 se. DPP increased as Fox activity increased (Fig. 5b), with a 19.6% chance of surviving 30 days on sites with low Fox activity compared with 1.6% on sites with high Fox activity at the average date when chicks hatch (15 May). Chick age as a control factor was also included in the top model with a positive effect on DPP ($\beta = 0.28 \pm 0.16$ se).

The proportion of Fox-, mustelid- and raptor-specific (though not all-avian predator) predation events was positively related to the activity of each predator group on a site-year level (linear regression on percentage of chicks predated by a predator transformed using $\arcsin(\sqrt{x})$: Fig. 6; all-avian: $F_{1,15} = 0.004$, $P = 0.95$). As predator activity increased on a site, the proportion of chicks predated by that predator also increased.

DISCUSSION

Our results demonstrate that although diurnal predation was biologically more significant than

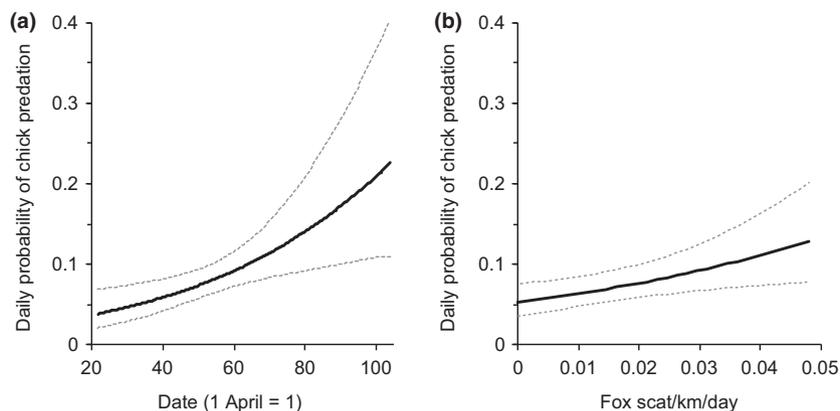
nocturnal predation, it was less intensive, and mammalian rather than avian predators had the highest impact on wader chick survival. Mammalian predation was of equal biological significance to diurnal predation because mammals were active both nocturnally and diurnally, whereas avian predators were only active by day. Foxes were most commonly implicated in mammalian predation events, whereas raptors were mainly responsible for avian predation. ARTS were a cost-effective tool for monitoring predation (Appendix S2) and should be considered for use in future predation studies. Detecting timing of predation was possible for 60% of chicks, and where timing could not be determined accurately this was largely because chicks moved out of range and were predated before ARTS could be moved. Importantly, the timing of predation could be determined for 58% of all tags that were never recovered and for which all predator inference information would otherwise have been lost (Table S3). This, combined with remain recoveries (Tables S3 and S4), made predator inference possible for 65% of all predation events (Table 3).

The predation mortality we recorded (87% of chicks) is higher than that reported by other studies in similar habitats (Table S6). We also found similarly high predation mortality (83%) attributed to the same predator species groups for 23 Common Redshank chicks we monitored

Table 4. Model selection results from binomial GLMMs testing for effects of predator activity (Fox, avian, mustelid), chick age and monitoring date on the daily probability of chick predation.

Variable inclusion and coefficients of best fit models						Model selection					
(Intercept)	Fox	Avian	Mustelid	Date	Age	AICc	Δ AICc	w	logLik (df)	R^2_m	R^2_c
-2.45 ± 0.13	0.31 ± 0.12			0.39 ± 0.14	0.28 ± 0.16	910.3	0.0	0.24	-448.1 (7)	0.00006	0.00006
x	x	x		x	x	910.7	0.4	0.19	-447.3 (8)	0.00008	0.00008
x	x		x	x	x	911.4	1.1	0.14	-447.7 (8)	0.00008	0.00008
x	x	x	x	x	x	912.1	1.8	0.10	-447.0 (9)	0.00016	0.00033
-2.48 ± 0.11	0.28 ± 0.10			0.36 ± 0.11		912.1	1.8	0.10	-450.0 (6)	0.04883	0.05715
x	x	x		x		912.8	2.5	0.07	-449.4 (7)	0.04540	0.04540
x	x		x	x		913.5	3.2	0.05	-449.7 (7)	0.04477	0.04477
-2.42 ± 0.16				0.41 ± 0.15	0.29 ± 0.15	914.2	3.9	0.03	-451.1 (6)	0.00004	0.00004
x	x	x	x	x		914.3	4.0	0.03	-449.1 (8)	0.04555	0.04555
x		x		x	x	915.8	5.5	0.02	-450.9 (7)	0.00004	0.00004
x			x	x	x	916.2	5.9	0.01	-451.1 (7)	0.00004	0.00004

Δ AICc, difference in AICc between a model and the model with the lowest AICc; w, AICc weight; logLik, log likelihood; df, number of estimable parameters. Shown are models within 6 Δ AICc units of that with the lowest AICc, with the best fit models (those which are not more complex versions of a simpler nested model of lower AICc value; Richards *et al.* 2011) highlighted grey, darker shading indicating the top model (that with lowest AICc). x denotes variables inclusion in each model, with standardised regression coefficients (betas \pm se) presented for variables included in the best fit models. Marginal (R^2_m) and conditional (R^2_c) estimates of model fit are calculated following Nakagawa and Schielzeth (2013). See Table S5 for results from the full model set.

**Figure 5.** Relationships between the daily probability of chick predation (DPP) and (a) monitoring date and (b) Fox activity at the average chick hatch date based on coefficients reported by the top model (Table 4). Solid lines are back-transformed logit predictions assuming a constant value (mean chick age, mean Fox activity or mean hatch date) for model covariates not represented in each plot. Dotted lines are 95% confidence intervals estimated using the delta method.

using the same methods as for Lapwing (five site-years; Table S7). These high predation rates are unlikely to result from misclassification resulting from scavenging or tag failure. Evidence of scavenging would have been present in ARTS data, exhibiting an unexpected tag signal reduction or disappearance after death when signals are impeded by vegetation, followed by a sharp increase and eventual disappearance upon scavenging when tagged remains were moved, lifted,

removed from site or destroyed. Tag failures were unlikely to have been misclassified as predation events: few tags failed before the full 30 days of monitoring (1% of 179 tags) and no additional tag failure went undetected because in all other cases any loss of tag signal from ARTS or manual telemetry was accompanied by observations of last known brood locations which confirmed true disappearance of an active chick, and therefore predation or death.

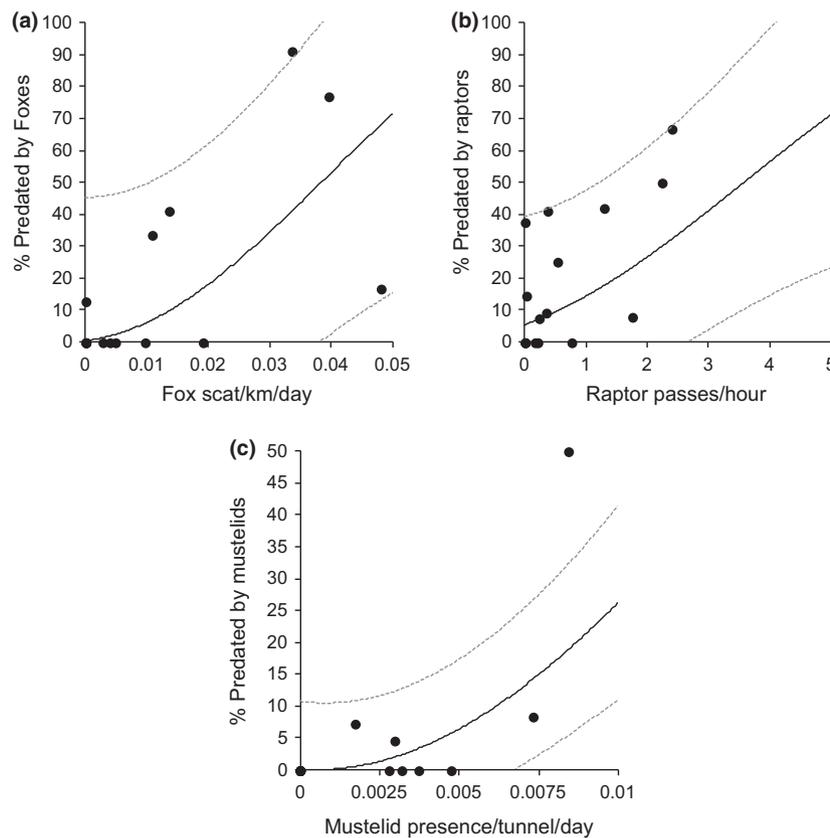


Figure 6. Relationships between the percentage of predated wader chicks predated by Foxes, raptors and mustelids and the activity of (a) Foxes ($F_{1,13} = 12.02$, $P = 0.004$), (b) raptors ($F_{1,15} = 8.68$, $P = 0.01$) and (c) mustelids ($F_{1,14} = 16.65$, $P = 0.001$), respectively, in each site-year. Solid lines are back-transformed predictions from univariate linear regression models on response variables transformed using $\arcsin(\sqrt{x})$. Dotted lines are 95% confidence intervals estimated using the delta method. Note that scales vary.

It is also unlikely that the use of ARTS themselves inflicted any additive predation mortality. The antenna and pole were too thin to provide a viable perch for avian predators and, when erected, the equipment was visually unobtrusive and unlikely to cause disturbance to breeding waders (Fig. S1). Frequent visits to download ARTS data (every 2–3 days) may have influenced mortality through human disturbance, although visits were no more frequent than during a conventional manual telemetry study (e.g. 1–5 days: Teunissen *et al.* 2008). However, further research would be needed to exclude completely any ARTS effects.

Radiotagging and repeated trapping have the potential to influence chick mortality by encouraging poor body condition, increasing detection by predators or reducing the ability to escape. Sharpe *et al.* (2009) found that frequent disturbance associated with tracking and recapturing chicks, rather than the attachment of a tag itself, affected body

condition, but that a recapture frequency of greater than 8 days was sufficient to reduce this effect. By following this recommendation the chicks we monitored attained body condition equal to or better than expected for their age, and there was no significant difference in condition between tagged and untagged chicks (Table S8; Beintema 1994, Mason & Smart 2015). Tags and mounting methods themselves could have directly hindered movement or increased visibility to predators, although other studies found no effects on the predation probability of tagged vs. untagged chicks (Hönisch *et al.* 2008, Schekkerman *et al.* 2009), and we expect these effects to be minimal due to tags being small, light, covered with feathers to reduce visibility and with very thin, black pliable antennae. Despite the potential negative effects, radiotagging is still the only practical method of studying causes of wader chick mortality. Our tagging and recapture methods matched

those used by other studies (Table S7), meaning that the high predation rates we detected are at least likely to be valid in the context of existing wader chick predation research.

Nocturnal mammalian predation was attributed mainly to Foxes, whose increasing activity reduced the probability of daily chick survival. Foxes are also responsible for the majority of wader nest predation (e.g. Teunissen *et al.* 2008) and if Fox predation pressures are reduced on a site through exclusion or lethal control, both wader nest and chick survival increase (Bolton *et al.* 2007, Schifferli *et al.* 2009, Rickenbach *et al.* 2011, Malpas *et al.* 2013). The impact of Foxes on lowland wet grassland is perhaps unsurprising given the 'honeypot' nature of these sites for generalist predators (Seymour *et al.* 2003), attracting high densities of other common prey species (rodents, lagomorphs, galliforms) as a result of better habitat conditions and less intensive hunting and agricultural pressure. Lethal Fox control is now ubiquitous on or around lowland wet grassland sites managed for breeding waders in the UK, so the fact that Foxes still account for a high proportion of chick predation indicates that the current lethal control methods or the implementation of those methods is largely ineffective. Electric fencing or encouraging ecosystem resilience through the provision of habitats for alternative prey are likely to be more successful alternatives (Laidlaw *et al.* 2013, 2015, Malpas *et al.* 2013).

Generalist raptors (Buzzard, Marsh Harrier, Kestrel, Peregrine) were equal in importance to Foxes in the proportion of chicks predated, but the activity of all avian predators combined did not affect daily predation rates. We found no evidence of corvid or gull predation and little evidence these species were perceived as predation threats by waders on our study sites, despite their presence in higher numbers compared with raptors (mean passes per hour: corvids = 2.2 ± 0.68 se, gulls = 0.4 ± 0.17 , raptors = 0.9 ± 0.32 ; Table S1). It is also unlikely that predation events from these species occurred but went undetected, as no chick remains were ever recovered from typical areas of high gull or corvid activity (e.g. colonies or nesting locations). The validity of managing avian predation of chicks by direct means (lethal or non-lethal) therefore needs careful consideration, as any corvid or gull control is unlikely to influence wader chick survival (although lethally controlling crows can successfully improve wader nest survival at high crow densities; Bolton

et al. 2007). Raptors are legally protected in the UK (Redpath *et al.* 2001) so non-lethal or indirect predation management methods would be the only options to manage unsustainable predation from these species.

We recorded a higher proportion of nocturnal, mammalian predation, particularly by Foxes, than did other chick-tracking studies, where avian predation was more important (Junker *et al.* 2004, Schoppenhorst 2004, Teunissen *et al.* 2005, 2006, 2008, Schekkerman *et al.* 2009). A limitation of these studies is the potential for a bias towards relocating avian-predated chicks (Teunissen *et al.* 2008, Schekkerman *et al.* 2009), which we found were easier (required less time) to locate than those predated by mammals. By recording the timing of predation, we were able to infer at least some predator-type information from the proportion of chicks whose remains were never found, which may explain the higher proportion of mammalian predation overall. These results also support the findings of predator control or exclusion studies which implicate mammals as more important chick predators (Bolton *et al.* 2007, Schifferli *et al.* 2009, Rickenbach *et al.* 2011, Malpas *et al.* 2013).

Another reason for the disparity may be differences in the activity of different predator types between regions. The studies where avian predation was found to be important were based in areas where Fox abundance may be low (grasslands along the North Sea coasts of The Netherlands and Germany; J. Bellebaum pers. comm.) while raptor abundance may be high. In contrast, studies which implicate mammals as important chick predators largely originate from areas where Fox abundance may be high while raptor abundance is low (UK, Switzerland: Bolton *et al.* 2007, Schifferli *et al.* 2009, Rickenbach *et al.* 2011, Malpas *et al.* 2013). Given the relationship we found between the proportions of chicks predated by Foxes and raptors and their respective activity (Fig. 6), the contrasting Fox and raptor predation results from these different regions may not be surprising. The higher level of mammalian predation found in this study is likely to be more representative of levels of mammalian predation on wet grassland sites managed for breeding waders in the UK.

Nevertheless, caution is required when interpreting the relative importance of predator types due to the possibility of misclassifying predated remains. However, the fact that the high proportion of nocturnal, mammalian predation we

detected by recording timing of predation information also matches the known importance of nocturnal, mammalian predation in limiting wader nest survival in the same habitat (Teunissen *et al.* 2008, Eglinton *et al.* 2009) gives further weight to the validity of our results, despite the disparity with previous chick predation studies.

The predator monitoring methods we used are cheaper and quicker than monitoring wader chicks themselves. Site managers could use such monitoring as a basis for rapid assessment of the likely importance of Foxes, mustelids and raptors in limiting wader chick survival on a site based on the relationships we found between the activity of these predator groups and the proportion of chicks predated by those predators (Fig. 6). Interpreting these relationships requires caution, however, due to the possibility of expectation-driven bias from observers who collected both predator activity and interpreted predated remains. We attempted to lessen such a bias by collating and inspecting the interpretation of chick histories and predated remain characteristics at the end of the project, although some possibility of bias still remains. It is also important to note that these relationships were found specifically for Foxes, small mustelids and raptors, which were the predator groups most active in predating waders and which elicited an anti-predator response from Lapwing adults on our study sites: they are unlikely to be relevant for or extendable to other predator species.

Chick mortality increased as the breeding season progressed, with later-hatching chicks susceptible to a higher daily risk of predation. Predation pressures are likely to increase seasonally as predators start to provision their own young, despite simultaneous increases in alternative prey. Over 50% of wader chicks monitored during this study hatched between 18 April and 15 May, the same period in which Fox cubs are developing (born March–April; e.g. Webbon *et al.* 2004) and raptor chicks hatch (May onwards for Marsh Harrier, Kestrel, Buzzard; Ferguson-Lees & Christie 2001). Early wader breeding attempts may be more likely to evade predation at the chick stage, and may be more likely to result in successful fledging. Juveniles fledging earlier in the season will also have a longer period in which to increase their body weight before winter, and may be more likely to survive to recruit to future breeding populations by having more time to locate suitable winter habitats and to learn key foraging and roosting

behaviours (Gill *et al.* 2014). Habitat and predation management methods that encourage successful early nesting attempts are therefore more likely to maintain populations and promote more rapid wader population recovery.

Managing chick predation is only likely to be advantageous on sites where this is the main mortality factor and where additional mortality has been minimized through good habitat management (Bolton *et al.* 2007, Eglinton *et al.* 2010, Mason & Smart 2015). Even on well-managed sites, we highlight the need for accurate knowledge about the timing of predation and activity of all wader chick predator groups to make meaningful inferences about the relative importance of different predators. The previously unproven importance of difficult-to-detect mammalian predation in wader chick mortality emphasizes the need to avoid making assumptions about predation based on visual observations of predator abundance or predation events alone. Predation pressures from key predator groups are likely to increase as predators increase across Europe (Foxes: Chautan *et al.* 2000, raptors: PECBMS 2014). A positive message is that the relationships we found between the proportions of chicks predated by Foxes, raptors and mustelids and the activity of these groups could be used with caution to indicate the likely relative importance of these predators on sites similar to those we studied.

We thank Thomas Bodey, Janine Bicknell, Tessa Cole, Maureen Gibson, Rebecca Laidlaw, Andrea Mason, Peadar O'Connell, Jean Roberts, Andrew Robertson, Leila Walker, Leah Williams and RSPB staff/volunteers for fieldwork, and Braides Farm, Lathwaite Farm, Gavin Thomas, Richard Storton and Karen Birkby for site access. All ringing and tagging was conducted under licence from the British Trust for Ornithology. Licences to disturb and handle birds were granted by Natural England and Scottish Natural Heritage for scientific research in line with the UK Wildlife and Countryside Act 1981. Adam Butler and Mark Brewer (BIOSS) provided statistical guidance, and Jochen Bellebaum, Christian Rutz, Ruedi Nager and three anonymous referees provided constructive comments on the manuscript. This study was jointly funded by the RSPB and Natural England through the Action for Birds in England Partnership.

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Received 19 May 2015;
revision accepted 26 July 2017.
Associate Editor: Christian Rutz.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Photographs of a typical ARTS set-up.

Table S1. Avian predators found on lowland wet grassland.

Table S2. Site-year specific chick survival estimates.

Table S3. Recovery rates of remains from predated chicks.

Table S4. Percentages of recovered tags attributed to different predator types.

Table S5. Full results of AICc model selection.

Table S6. Mortality statistics compared between wader chick survival studies.

Table S7. Predation summary for Redshank chicks monitored with Lapwing chicks.

Table S8. Body condition indices for tagged and untagged Lapwing chicks.

Appendix S1. Detection of predation and diel patterns of signal strength in ARTS data.

Appendix S2. Cost-benefit analysis of ARTS.