Title: Diversionary feeding as a means of reducing raptor
predation at seabird breeding colonies

Authors: Jennifer Smart, Arjun Amar

PII: S1617-1381(18)30131-6
DOI: https://doi.org/10.1016/j.jnc.2018.09.003
Reference: JNC 25664

To appear in:

Received date: 13-4-2018
Revised date: 10-9-2018
Accepted date: 10-9-2018

Please cite this article as: Smart J, Amar A, Diversionary feeding as a means of reducing raptor predation at seabird breeding colonies, *Journal for Nature Conservation* (2018), https://doi.org/10.1016/j.jnc.2018.09.003

Diversionary feeding as a means of reducing raptor predation at seabird breeding colonies

Short title: Diversionary feeding to reduce raptor predation on seabirds

Jennifer Smart[a,b] and Arjun Amar[a]

[a] RSPB Centre for Conservation Science, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK

[b] School of Biological Science, University of East Anglia, Norwich, Norfolk, NR4 7TJ, UK

Corresponding author:

Jennifer Smart: Jennifer.smart@rspb.org.uk

Arjun Amar: arjundevamar@gmail.com

Present address: Fitzpatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7701, Cape Town, South Africa

Abstract

Predation can limit bird populations, especially in ground-nesting and colonial species. Solutions are usually available to reduce the impacts of predation if the predator is non-native or not legally protected (e.g. predator control or exclusion). However, when the predator is protected by law (e.g. raptors) potential solutions are limited. If predator and prey are both species of conservation concern this can bring the conservation of these species into conflict. Diversionary feeding (DF) is a potential solution, whereby predators are provided with food to reduce their motivation to hunt. The efficacy of DF has rarely been tested thus, in this paper, we test the efficacy of DF to reduce predation by kestrels, *Falco tinninculus,* a protected and declining raptor, on little tern chicks, *Sternula albifrons*, a protected seabird, within an internationally important colony in eastern England. We used a 17-year dataset of annual estimates of little tern productivity and counts of kestrel predation events to compare years with and without DF (DF = 6 years). During a four-year period of more intensive monitoring efforts, where we employed DF at focal kestrel nests in alternate years, we quantified the rates of kestrel predation at the colony and prey provisioning rates at kestrel nests. Predation rates were 47% lower and productivity of little terns doubled in years when kestrels were fed. Intensive monitoring showed that predation rates by kestrels at the colony were 88% lower in the two years when kestrels were fed. Provisioning rates of all wild prey and little tern prey, was 3.4 and 6.2 times lower in DF years and the likelihood of little tern chicks being provisioned at nests was lower when alternative wild prey were provisioned. DF is an effective tool to reduce predation and increase productivity of little tern colonies threatened by kestrel predation. The magnitude of these effects on little tern productivity was sufficient to promote population increases. Raptor conservation has resulted in increasing populations of many species and it is expected that predator-prey conflicts is likely to increase. DF could be an important tool to manage these conservation issues, but further tests of the efficacy in different predator-prey systems will be needed.

Keywords: Little Tern, *Sternula Albifrons*, Kestrel, *Falco tinnuculus,* alternative prey, conservation conflict

Introduction

In human modified landscapes, conservation conflicts are becoming increasingly common (Kubasiewicz, Bunnefeld, Tulloch, Quine, & Park, 2016; Redpath, et al., 2013) and can occur when a predator of conservation concern preys on another species of conservation concern, with consequent detrimental effects on the survival or breeding success of the prey species (Smart & Ratcliffe, 2000; Summers, Willi, & Selvidge, 2009). Predation can limit populations of some species, in particular those that are ground-nesting, colonial, range-restricted because of severe population declines and those that are long lived with slow reproductive rates (Newton, 1998; Roos, Smart, Wilson, & Gibbons, 2018). When the main predator is non-native and/or not protected by law, predator removal can be effective at increasing hatching success, fledging success and breeding populations of the prey species (Smith, Pullin, Stewart, & Sutherland, 2010). When the predator is mammalian, predator exclusion can lead to increases in hatching success (Smith, Pullin, Stewart, & Sutherland, 2011). However, where the predators themselves are protected (e.g. raptors or protected mammals), the range of potential solutions to reduce their predatory effects on species of conservation concern is extremely limited and rarely tested. Methods to reduce predation have produced mixed results which are often short-lived and have small-scale application e.g. visual, physical or sonic deterrents, chemical repellents or conditioned taste aversion (Smith, Linnell, Odden, & Swenson, 2000).

Effective raptor conservation, through decreased persecution, recovery from deleterious effects of pesticides and reintroductions (Evans, et al., 2009; Newton, 1998; Smart, et al., 2010), has led to increases in populations of many raptor species in the UK. For example, buzzards *Buteo buteo* and red kites *Milvus milvus* increased by 84 and 1,231% respectively between 1995 and 2015 (Harris, et al., 2017). The combined effect of increasing predator populations alongside a decline in the abundance and distribution of their key prey species increases the likelihood of negative effects on prey species that are themselves of conservation concern. It is thus increasingly important that effective, legal and ethical solutions are developed and tested which can reduce predation pressures in circumstances where predator and prey species are both of conservation concern.

Diversionary feeding (DF) is one potential solution to such conservation conflicts. DF is defined as "the use of food to divert the activity or behaviour of a target species from an action that causes a negative impact, without the intention of increasing the density of the target population" (Kubasiewicz, et al., 2016). DF might work because it is likely to reduce the motivation of the predator to hunt natural prey. In a review of the effectiveness of DF as a strategy to reduce conflicts involving wildlife (including both human-wildlife and conservation conflict), Kubasiewicz et al. (2016) found there were relatively few studies (n = 30), that success varied between studies and that only 13 studies were sufficiently detailed to allow quantification of effectiveness. Furthermore, only three of the studies related to reducing predatory effects on prey species of conservation concern and only one of these quantified effectiveness (Smart & Ratcliffe, 2000).

In the UK, there is now a growing range of conservation conflicts where DF may provide a solution e.g. pine martens *Martes martes* preying on capercaillie *Tetrao urogallus* nests (Summers, et al., 2009), raptors preying on grey partridges *Perdix perdix* (Watson, Aebischer, Potts, & Ewald, 2007; Watson, Aebischer & Cresswell, 2007) and Eurasian kestrels *Falco tinninculus* preying on little tern chicks, *Sternula albifrons* (Smart & Ratcliffe, 2000). Given the growing range of conservation conflicts and the paucity of scientific evidence for the efficacy of this technique, there is an urgent need to test the efficacy of DF across a range of predator-prey systems, in order to understand the success and generality of this approach. Each example is likely to have specific practical limitations, in terms of the ability to target food at the individuals in a population causing the conflict, while at the same time limiting possible negative side-effects of DF, such as increased productivity, survival and potentially population size of the target predator species (e.g. Dijkstra, Vuursteen, Daan, & Masman, 1982; Hansen, 1987; Wiehn, Ilmonen, Korpimaki, Pahkala, & Wiebe, 2000) or food being taken by non-target species (Redpath, Thirgood, & Leckie, 2001).

In this paper, we focus on the Eurasian kestrel (hereafter kestrel) and little tern conservation conflict. The little tern is Britain's second rarest seabird and is protected under Schedule 1 of the Wildlife and Countryside Act 1981 and listed under Annex I of the EC birds directive (Batten, Bibby, Clement, Eliot, & Porter, 1990). Little terns are 'Amber' listed in the Birds of Conservation Concern (Eaton, et al., 2015). The species is a colonial beach-nesting seabird that has declined by 25% between the mid-1980s and the late-1990s (Mitchell, Newton, Ratcliffe, & Dunn, 2004), with further declines recorded from 2,153 pairs (1998-2000) to 1,417 pairs (2006; Mavor, Heubeck, Schmitt, & Parsons, 2008). Declines in this species are thought to be due to successive years of poor productivity, which have been influenced, in order of apparent importance, by predation, tidal flooding, weather, disturbance and poor food availability (Ratcliffe, 2003). It is a species which largely depends upon conservation action and a combination of 24-hour protection from wardens and/or electric fencing can be extremely effective at reducing effects of predatory mammals (largely red fox *Vulpes vulpes*, hedgehogs *Erinaceus europaeus* and domestic cats *Felis silvestris*) and human disturbance (Smart, 2003). However, predation of little tern chicks by kestrels, a protected and declining raptor species in the UK (-38% 1995-2015; Harris, et al., 2017), has limited the success of little terns at a number of important colonies, including one of the UK's largest, at Great Yarmouth (Thompson, Brindley, & Heubeck, 1997). In 2006, 369 pairs nested within this colony, which was 26% of the UK population (1,417 prs; Mavor, et al., 2008) and 0.7-1.1% of the European population (35-55,000 prs; BirdLife International, 2004). DF of kestrels has been employed at this site periodically since 1995 (Fig. 1). With the increasing importance of this colony in a UK and EU context, and the increasing numbers of other colonies reporting kestrel predation issues, it became critical to examine DF as a tool to reduce the effects of kestrel predation on little terns.

In this paper, we report on analyses of a 17-year dataset of annual estimates of little tern productivity and counts of kestrel predation events, to compare between years with and without DF (DF = 6 years), coupled with a four-year period of a more formal experiment when we employed DF at focal kestrel nests in alternate years (2006 and 2008) and quantified the kestrel predation rates at the colony and prey provisioning rates at kestrel nests. Our main hypothesis was that kestrels would predate or provision fewer little tern chicks in years when they were provided with DF and that this would lead to higher little tern productivity. This hypothesis was tested by addressing the following questions:

1. Were annual counts of kestrel predation events lower and little tern productivity higher in years when kestrels were fed diversionary food?
2. Was kestrel predation at the little tern colony lower when focal kestrel nests were fed diversionary food?
3. Was provisioning of little terns and other wild prey at kestrel nests reduced when they were fed diversionary food?

Materials and methods

Study system

This study focused on the little tern colony located in Great Yarmouth in eastern England, UK (Latitude 52.627150, Long 1.7459035) and kestrels nesting within ~3km of that colony (Fig. 2).

1. Were annual counts of kestrel predation events lower and little tern productivity higher in years when kestrels were fed diversionary food?

We extracted long-term annual data on little tern population size, productivity, the number of little tern chicks predated by kestrels and whether DF occurred or not from the annual colony reports (1986-2009; Fig. 1). These reports were compiled by the wardens and volunteers, who were on site 24 hours a day, 7 days a week for the duration of the breeding season, to protect the little tern colony and to record data about the breeding success of little terns and the causes of nest and chick failure. The number of little terns incubating nests were counted every 2 to 3 days and population size was measured as the peak number of nests each year. Productivity was estimated from daily counts of fledglings present at the colony, and the peak count of fledglings divided by population size gave an annual measure of the number of little tern chicks fledged per pair. Thus, productivity is a colony measure, not an individual nesting attempt measure. The number of little tern chicks predated by kestrels was recorded by wardens and volunteers who observed kestrels visiting the colony during routine patrols of the colony perimeter or when alerted to the presence of a predator at the colony by the alarms and mobbing behaviour of the little terns. These annual counts of kestrel predation are minimum estimates because kestrel predations events will have been missed and it was not always possible to be sure if a strike by a kestrel was successful when little tern chicks were very young. In our analysis, we excluded seven years from this dataset because i) kestrels only became a significant problem (>50 tern chicks predated) in 1989 hence 1986-1988 were excluded, ii) in 2000, DF was only used for part of the season so we could not assign this year to a specific DF category and iii) between 2002 and 2004, there were significant disturbance events at the colony which prevented the terns from settling to nest or caused catastrophic failure of the colony. This resulted in data on annual productivity and kestrel predation for 11 years without DF and six years with DF.

2. Was kestrel predation at the little tern colony lower when focal kestrel nests were fed diversionary food?

In 2006 we instigated four years of more intensive monitoring coupled with a more formal DF experiment, where DF occurred in alternate years (2006 and 2008). We employed a researcher, to find, feed and monitor provisioning rates at kestrel nests and to undertake timed watches for kestrel predation at the colony. The researcher completed a single timed watch of ~2hours, focused specifically on this task, on between 61% and 100% of days during the tern chick rearing period depending on the year (mean ± SE timed watch length = 144 ± 4 mins; % days each season: 2006 = 61%, 2007 = 86%, 2008 = 85%, 2009 = 100%). To account for possible diurnal patterns in hunting behaviour, days were split into four 4-hour time periods starting at 05:00, 09:00, 13:00 and 17:00 and we aimed to make at least four timed watches per time period each year. There was very little diurnal variation in hunting pressure and each time period received on average 9.1 ± 5.7 (SD) timed watches per year (Supplementary information 1).

3. Was provisioning of little terns and other wild prey at kestrel nests reduced when they were fed diversionary food?

During the intensive monitoring years (2006-2009), we monitored provisioning rates of prey at a total of three kestrel nests located within 3km of the little tern colony and provided the birds using these nests with diversionary food in 2006 and 2008. Locating kestrel nests began in early May which coincided with the average first clutch laying date (1 May; Joys & Crick, 2004) and were found mainly by checking traditional nest sites, but also by searching suitable habitats for any evidence of breeding kestrels. Over the four years, three kestrel nests, named Racecourse (1.1km from colony), Cemetery (1.4km) and Stadium (1.7km), were located and monitored for two (2006-07), one (2008) and two (2008-09) years respectively and Racecourse 2006, Cemetery 2008 and Stadium 2008 were subjected to DF (Fig. 2). While the number of kestrel nests is small, this is typical of the number of pairs of kestrels that might be expected, given the geographical circumstances of this conservation conflict (colonial seabird with limited kestrel nesting opportunities in the vicinity). No other kestrel nests were located within the search area and the presence of breeding pairs from unknown nests is unlikely because our nest-searching was thorough and there was no evidence of kestrels departing from the colony with prey in a direction that was inconsistent with the pairs we were monitoring. Supplementary Information provides more detailed information on the kestrel nest monitoring (SI Page 2).

Once a kestrel nest was located, and permission was granted for access to monitor and erect nest cameras and to provide DF, we began feeding and monitoring. DF was provided twice daily (~08:00 and ~16:00), these timings being a trade-off between feeding the kestrels as early in the day as possible, ensuring a consistent supply of DF and having feed times that could be achieved by one member of staff. DF was placed within 5 m of the nest entrance using a ledge, preferably an existing one, but where necessary one was erected. Kestrel nests were provided with a mixture of dead laboratory mice (mean 42.3% ± 0.02) and dead day old poultry chicks. Food was purchased frozen (www.frozendirect.com) but provided to the kestrels thawed. We aimed to provide each fed kestrel nest with 100% of the daily requirements based on the number and age of kestrel chicks (SI Page 3). However, the amount of food provided was variable, ranging from 52-322% of weekly needs, with 100% or more provided on 82% of the weeks. Where possible, excess food was removed from ledges to prevent build up but this only equated to 7% of mice and 3% of poultry chicks. Exact details of the DF including total and daily costs can be found in SI (Page 4).

To determine the delivery rates of prey and, in particular little tern chicks to kestrel nests in years with and without DF, kestrel nests were monitored using miniature nest cameras (Bolton, Butcher, Sharpe, Stevens, & Fisher, 2007). Prey were categorised as little tern chicks, diversionary food (mice & poultry chicks), wild mammals, other birds, and unidentified. Nest cameras were mounted in the best location possible to record the identity of prey being delivered to kestrel chicks during daylight hours but, without using multiple cameras, it was impossible to position the camera to capture identifiable images of every prey item because of the variable nature of circumstances at each kestrel nest and how prey items were delivered to the nest. This resulted in a variable percentage of prey items being precisely identified (Racecourse 2006 = 70%; Racecourse 2007 = 43%; Cemetery 2008 = 79%; Stadium 2008 = 97%; Stadium 2009 = 35%). To supplement the camera data, visual observations of prey delivery at kestrel nests by researchers overlapped with camera monitoring on 54% of days and were on average 118 ± 3 minutes in length and time of day was varied. Observations involved watching from a location where nests could be observed without affecting the kestrels. Attempts to observe and identify prey being brought to the nest used a combination of binoculars and a telescope, mounted on a tripod, trained on the kestrel nest (binoculars 8x42, telescope 25-60x). Data from cameras gave a more complete picture (99 days, daylight hours; number of identified/unidentified prey = 596/444). However, researcher observations did supplement the camera data by adding identifiable prey that would otherwise have been recorded as unidentified by the cameras (cameras + observations; number of identified/unidentified prey = 643/448).

Analytical methods

1. Over the longer term, were annual counts of kestrel predation events lower and little tern productivity higher in years when kestrels were fed diversionary food?

As the number of pairs of little terns (COLONY SIZE) varied between years and this might affect the availability of little tern chicks to kestrels or the number available to fledge, we divided the annual counts of the number of kestrel predation events and the number of little tern chicks fledged by the COLONY SIZE. We used two sample t-tests (with unequal variance) to assess whether the number of little tern chicks i) predated by kestrels per little tern pair and ii) successfully fledged per little tern pair, varied between years with and without DF.

In all subsequent analyses relating to our intensive monitoring years, we were specifically interested in effects of DF. However, we needed to control for non-linear seasonal patterns of predation at the colony that peak in mid-season (Smart & Ratcliffe, 2000), and for any differences in predation rates being affected by the annual availability of little tern prey. To control for these effects we included COLONY SIZE and the quadratic seasonal effect (SEASON DAY) which was defined relative to little tern chick hatching dates, with day 0 being the date on which the first little tern chick hatched (range in dates 18th – 26th June 2006-2009). The response variables were counts so we used a Generalised Linear Model fitted in SAS v9.4 (SAS Institute Inc., 2015) using the GENMOD function, with a Poisson distribution and a log link function. We accounted for any over-dispersion using the DSCALE function (scaled by the square root of deviance/DOF). In all cases, outputs for effects of DF were obtained through the back-transformation of least square means, with the statistical significance of differences between categories obtained using difference in least square mean tests.

2. Was kestrel predation at the little tern colony lower when focal kestrel nests were fed diversionary food?

To address this question we specified the following model. As daily timed watches varied in the length of time spent observing kestrel predation at the colony, we included this as an offset which effectively models the count as an hourly rate of predation.
Response variable: Number of little tern chicks predated by kestrels
Offset variable: Natural log (Length of timed watch)
Explanatory variables: DF + COLONY SIZE + SEASON DAY + SEASON DAY^2

3. Was provisioning of little terns and other wild prey at kestrel nests reduced when they were fed diversionary food?

To address these questions we specified two models: little tern prey model and wild prey model. In the little tern prey model, the number of zero counts (70.3%) necessitated the use of a zero-inflated Poisson model (Ridout, Hinde, & Demétrio, 1998). In addition, we suspected that when the delivery rate of other wild prey was high this would reduce the delivery rate of little tern prey, so we specifically modelled the probability of observing a zero count being conditional on the number of OTHER WILD PREY delivered.

Little tern prey model:
Response variable: Daily count of little tern chicks delivered to kestrel nests
Explanatory variables: DF + COLONY SIZE + SEASON DAY + SEASON DAY^2
+ OTHER WILD PREY

Wild prey model:
Response variable: Daily count of wild prey delivered to kestrel nests
Explanatory variables: DF + COLONY SIZE + SEASON DAY + SEASON DAY^2

Results

1. Were annual counts of kestrel predation events lower and little tern productivity higher in years when kestrels were fed diversionary food?

Over the 17 years since kestrel predation became a problem and when annual estimates of kestrel predation and little tern productivity are available, a minimum of 3436 little tern chicks were predated by kestrels (annual average = 202 ± 152 [SD]; min = 38, max = 526) and 2536 little tern chicks fledged (annual average = 149 ± 161 [SD]; min = 0, max = 673). Significantly higher numbers of little tern chicks were predated by kestrels in years without DF (Mean chicks pair^{-1} predated by kestrels [±SE]: noDF = 0.98 ± 0.20 n = 11, DF = 0.52 ± 0.16, n = 6, t_{15} = 1.86, P = 0.04). Little tern productivity was also higher in years when DF was provided (mean fledged chicks pair^{-1} [±SE]: noDF = 0.42 ± 0.13, DF = 0.88 ± 0.39, t_{15} = -1.55, P = 0.08). Although differences in productivity were not statistically significant, the difference is likely to be of biological significance because, with an average population size of 246 pairs (95% CI 216-276), these differences would result in 103 (91-116) little tern chicks fledging in years without DF compared to 216 (190-243) in years with DF.

2. Was kestrel predation at the little tern colony lower when focal kestrel nests were fed diversionary food?

During our more detailed monitoring years (2006-2009), we found strong effects of DF on kestrel predation rates, after controlling for seasonal and little tern colony size effects (Table 1). Significantly fewer little tern chicks were predated when kestrels were fed (Table 1; Fig. 3). Assuming a 16 hour day, these hourly rates of predation resulted in 9.1 (LCI-UCI: 7.0-11.8) little tern chicks predated per day during non DF years compared to 1.1 (0.6-2.1) during DF years.

3. Was provisioning of little tern and other wild prey at kestrel nests reduced when they were fed diversionary food?

During our more intensive monitoring years (2006-2009), three kestrel nests were monitored for two (2006-2007), one (2008) and two years (2008-2009) respectively. This resulted in 101 days of data on prey provisioning. A total of 1091 different prey items were recorded being provisioned at these nests of which 41.1% could not be identified to prey type. Of the prey identified (n = 643), 55.6% was diversionary food, 27.4% were mammals, 10.3% were little tern chicks and 6.7% were birds other than little tern chicks (Fig. 4). In the three kestrel nest year combinations when DF was deployed, diversionary food made up 60.8, 72.1 and 73% of the identifiable food items provisioned at the nests (Fig. 4).

The number of all wild prey (little terns, wild mammals and other bird species) provisioned to these kestrel nests each day was ~3.4 times higher during non-DF years and there were no significant seasonal or colony size effects (Table 1; Fig. 5). The number of little tern chicks provisioned was ~6.2 times higher during non-DF years and there were effects of season and other wild prey provisioned (Table 1; Fig. 5). The number of little tern chicks provisioned peaked in mid-season and declined in late season (Parameter estimates [Poisson model]: intercept = -0.98, season = 0.16, season^2 = -0.008). Little tern chicks were also less likely to be provisioned when many other wild prey were being provided and the magnitude of this effect was such that there was a ~60% chance that little terns featured in the daily diet when five wild prey were provisioned, declining to ~10% when 15 wild prey were provisioned (Parameter estimates [logit model]: intercept = 1.57, wild prey = 0.23).

Discussion

In this paper we test the efficacy of DF in a predator-prey system involving kestrels and little terns, and provide evidence that kestrels predate fewer little tern chicks from an internationally important colony and provision fewer little terns at their nests in years when diversionary food is provided at focal kestrel nests. All monitored kestrel nests successfully fledged chicks, irrespective of whether they were fed diversionary food or not, suggesting the breeding success of the predator in this system was not compromised nor boosted by feeding or monitoring. The reduction in kestrel predation in DF years resulted in improvements in little tern productivity that would be sufficient to increase the species' population and therefore likely to improve the conservation prospects of the prey species in this system. For example, using the hourly rates of kestrel predation (assuming a 16 hour day and 30 day chick period), we estimate that on average ~273 chicks are predated by kestrels in years with no DF compared to ~33 in DF years, and that annual estimates of little tern productivity were around twice as high in years with DF, accepting that estimates of productivity incorporate all causes of breeding season mortality on eggs and chicks. The geographical situation of this conflict, with a colonial beach nesting seabird and limited nesting opportunities for the predator, is likely to be typical of this conservation conflict so providing DF for a small number of kestrel pairs to benefit a relatively large number of threatened seabirds is a logistically feasible and biologically important solution.

There was a large discrepancy between the number of little tern chicks predated from the colony and the number observed being provisioned at focal kestrel nests. For example, during non-feeding years, we observed 44 little tern chicks provisioned at kestrel nests and 189 taken by kestrels from the colony (23%). There are a number of potential reasons for this discrepancy:

1. The estimates of little tern prey delivery at kestrel nests are minimum estimates because a proportion of the unidentified prey will have been little tern chicks. Applying the proportion of little tern chicks to the figure for unidentified prey then summing the known and estimated, means that ~37% of observed kestrel kills at the colony could have been delivered to monitored kestrel nests.
2. We have no way of knowing what proportion of little tern chicks are consumed by the adults. Adult kestrels need ~50 g food per day (SI Page 3). Given that there is variation in the distances different adult kestrels would need to fly between the colony and their nest (Fig. 2), the energy demands of the kestrel chicks varying over time and the energetic value of little tern chicks as prey varying between individual chicks and over time (little tern chicks mean ± SE mass (g): 1st July 2006 = 17.7g ± 0.7, n = 122, range = 8.1-43.6g; 8th July 2006 = 33.6g ± 0.6, n = 213, range = 7.8-49.8g; RSPB unpublished data), it is very likely that adult kestrels are constantly making decisions about which prey to consume in situ and which to take back to their chicks. It may be more energetically profitable for the adults to consume very small little tern chicks in situ. In this study adult kestrels were often observed landing a short distance from the colony and consuming little tern prey (J. Smart personal observation).
3. It is also possible that there were other unknown kestrel pairs or non-breeding individuals involved in predation at the colony. While we cannot rule out the possibility of non-breeding individuals, the presence of other breeding pairs is unlikely because our nest-searching was thorough and there was no evidence of kestrels departing from the colony with prey in a direction that was inconsistent with the pairs we were monitoring.

Given that the proposed mechanism through which DF should work is to reduce the motivation of the predator to hunt, then there is an expectation that diversionary food would also be consumed by the adult kestrels. While we had no way of directly monitoring consumption by adult kestrels, we do know exactly how much food was supplied and how much of that was observed being provisioned to the nests. We observed ~46% of the diversionary food being provisioned at nests (784 items taken: 358 observed) but a further 249 of the unidentified prey items may have been diversionary food given the proportions observed, which means that up to 77.4% of the diversionary food could have been provisioned to kestrel nestlings. This suggests that adult kestrels may have consumed around 20% of the diversionary food to meet their own needs. We also observed that provisioning of all wild prey was reduced when DF was provided and that provisioning of wild prey other than little terns affected the likelihood of little tern featuring in the diet, additional to the effects of DF. This suggests that overall hunting motivation was reduced in relation to the provision of diversionary food and that the kestrels preferred to provision their normal prey of wild mammals compared to little tern chicks. This could suggest that the defensive nature of little tern adults at colonies, when protecting their young, might mean that little tern chick prey represents a less accessible, more risky or dangerous prey type, that is only taken when very abundant or when the kestrels' normal mammal prey are not abundant.

It is therefore likely that the decisions made by kestrels, in terms of what and when to hunt, is a complex interaction between many competing requirements. These include i) the motivation to hunt, which is affected by the provision of DF, interacting with individual kestrel behaviour, as well as ii) the spatial and temporal variation of prey availability including small mammals, the main year-round prey of kestrels, and little terns, in relation to kestrel chick hatching and iii) the quality of hunting areas in the vicinity of kestrel nests, coupled with the distance that kestrels need to travel to hunt little terns. It is very likely that kestrels are simply exploiting food resources in relation to their availability and profitability at different times. Within this, DF acts as both a profitable and available food source that reduces their need to hunt, but does not completely eliminate the drive to hunt, which may be an inherent force within predators.

How general are these results in the context of other conservation conflicts?

Every predator-prey system will have particular factors relating to the species involved that need to be considered when designing a DF approach, such as what, where, when and how to provide DF, how much food to provide, how to minimise the amount of food being taken by non-target species, and when to start and finish feeding. There are some clear generalities that can be taken from this and other studies of DF, as a tool to reduce the effects of predators. In the case of DF raptors species, feeding them as close to their nests as possible fulfils a range of purposes: i) it allows targeting of only those individuals or pairs that are causing the conflict (Amar, Arroyo, Redpath, & Thirgood, 2004); ii) targeted individuals are more likely to find and adapt to using the food; iii) it allows feeding to occur for the absolutely minimum time needed to achieve the conservation aim; iv) non-target species are less likely to approach the vicinity of a raptor nest, in our study magpies only took food from near kestrel nests once the kestrel chicks had fledged, presumably because the threat of attack from adult kestrel diminishes at this time; and v) it is easier to monitor the species' use of the diversionary food. However, it may not always be possible to feed close to the nest, for example if it is unsafe to do so, if the landowner refuses access, if the nest site is inaccessible or the target species is prone to disturbance. In these circumstances the options for feeding will then very much depend on the target species and their ecology.

Using the right type of diversionary food (size and species) for the target species, being consistent about the timing and frequency of feeding, and aiming to provide around 100% of their requirements, given the number and age of offspring and adults, are all factors that are likely to improve the success of any DF programme. Prior to this study, the efficacy of DF has only been tested in relation to a very limited number of conservation or game management scenarios; hen harriers and red grouse (Redpath, et al., 2001), buzzards and released gamebirds (Parrott, 2015), striped skunk *Mephitis mephitis* and ducks (Greenwood, Pietruszewski, & Crawford, 1998) and northern racoon *Procyon lotor* and ground nesting birds (Storey, 1997). Although DF is often considered an expensive option, few studies report any analyses of cost-effectiveness (Kubasiewicz, et al., 2016). In our study, the main costs were employing a project assistant for 3 months to find, feed and monitor nests (c. £12,000) with the additional cost of diversionary food (£100-200 per nest). If DF was applied within our system purely for conservation purposes (i.e. without the associated monitoring of this study), the costs would be considerably less.

Main Conclusions

DF using the methods deployed in this kestrel and little tern predator-prey study system, is a successful tool to improve the conservation prospects of little terns. The reduction in kestrel predation and subsequent improvements in little tern breeding success were sufficient to increase productivity and, subject to other pressures, could in the long term promote population increase of this threatened seabird. Given the costs involved with running a successful DF programme, we suggest i) DF should only be used when there is a justifiable conservation need, for example, when predation rates are sufficient to reduce the success of the prey population to levels that are likely to cause population decline and ii) targeting this method towards larger seabird colonies will bring the biggest benefit for conservation and we provide some key methods that others could follow (SI Page 5). It is relatively easy to consider when there is a justifiable conservation need to introduce DF but it is more difficult to describe circumstances in which you might cease to DF, because in most situations once an individual predator has found a reliable, profitable prey source it is unlikely to stop using it. However, there may be individual variation in the exploitation of prey resources so the need for DF could decline when natural mortality removes particular individuals from the population. In addition, if the predator is limited by something else, for example nest sites or survival, which prevents predator numbers from increasing while prey numbers increase, due to the success of the DF, then the impact of predator on prey may decline over time to such an extent that the conservation justification for DF no longer applies.

Many species of raptors are rapidly increasing in distribution and abundance thanks to successful conservation programmes that led to the removal of dangerous pesticides from the landscape, reductions in illegal killing and successful reintroductions programmes (Deinet, et al., 2013). However, many of the groups of birds that are limited by predation, for example waders, gamebirds and seabirds (Roos, et al., 2018), continue to decline. This means there is an increasing likelihood for future conservation conflict between protected raptors and species of conservation concern. DF could become an increasingly important tool to reduce these conflicts but further tests in different predator-prey systems, with species that differ in their ecological needs, are necessary to ensure consistency of effectiveness across the range of potential applications.

Acknowledgements

We would like to thank the many RSPB staff and volunteers who have been involved with managing and monitoring the little tern colony at Great Yarmouth. Sarah Lewis, Charlie Cliffe and Henrietta Bellman for their dedication in finding, feeding and monitoring kestrels. Allan Drewitt, Phil Whitfield, Graham Appleton and an anonymous referree for comments on the manuscript.

Funding

This work was funded by the RSPB with support from Natural England’s Action for Birds in England funding stream.

References

Amar, A., Arroyo, B., Redpath, S., & Thirgood, S. (2004). Habitat predicts losses of red grouse to individual hen harriers. *Journal of Applied Ecology, 41*, 305-314.

Batten, L. A., Bibby, C. J., Clement, P., Eliot, G. D., & Porter, R. F. (1990). *Red Data Birds in Britain*: T. & A.D. Poyser, London.

BirdLife International. (2004). Birds in Europe: population estimates, trends and conservation status. In *BirdLife Conservation Series No.12*. Cambridge: BirdLife International.

Bolton, M., Butcher, N., Sharpe, F., Stevens, D., & Fisher, G. (2007). Remote monitoring of nests using digital camera technology. *Journal of Field Ornithology, 78*, 213-220.

Deinet, S., Ieronymidou, C., McRae, L., Burfield, I. J., Foppen, R. P., Collen, B., & Böhm, M. (2013). Wildlife comeback in Europe: The recovery of selected mammal and bird species. Final report to Rewilding Europe by ZSL, BirdLife International and the European Bird Census Council. 308 pp. . In. London, UK.: Rewilding Europe.

Dijkstra, C., Vuursteen, L., Daan, C., & Masman, D. (1982). Clutch size and laying date in the kestrel *Falco tinnunculus*: effect of supplementary food. *Ibis, 124*, 210-213.

Eaton, M. A., Aebischer, N. J., Brown, A. F., Hearn, R. D., Lock, L., Musgrove, A. J., Noble, D. G., Stroud, D. A., & Gregory, R. D. (2015). Birds of Conservation Concern 4: the population status of birds in the United Kingdom, Channel Islands and Isle of Man. *British Birds, 108*, 708-746.

Evans, R. J., Wilson, J. D., Amar, A., Douse, A., Maclennan, A., Ratcliffe, N., & Whitfield, D. P. (2009). Growth and demography of a re-introduced population of White-tailed Eagles *Hallaeetus albicilla*. *Ibis, 151*, 244-254.

Greenwood, R. J., Pietruszewski, D. G., & Crawford, R. D. (1998). Effects of food supplementation on depredation of duck nests in upland habitat. *Wildl Soc Bull, 26*, 219-226.

Hansen, A. J. (1987). Regulation of Bald Eagle Reproductive Rates in Southeast Alaska. *Ecology, 68*, 1387-1392.

Harris, S. J., Massimino, D., Gillings, S., Eaton, M. A., Noble, D. G., Balmer, D. E., Procter, D., & Pearce-Higgins, J. W. (2017). The Breeding Bird Survey 2016. In *BTO Research Report 700*: British Trust for Ornithology, Thetford.

Joys, A. C., & Crick, H. Q. P. (2004). Breeding periods for selected bird species in England. In *BTO Research Report No. 352*. British Trust for Ornithology, Thetford, UK.

Kubasiewicz, L. M., Bunnefeld, N., Tulloch, A. I. T., Quine, C. P., & Park, K. J. (2016). Diversionary feeding: an effective management strategy for conservation conflict? *Biodiversity and Conservation, 25*, 1-22.

Mavor, R. A., Heubeck, M., Schmitt, S., & Parsons, M. (2008). Seabird numbers and breeding success in Britain and Ireland, 2006. In *UK Nature Conservation, No. 31*. Peterborough: Joint Nature Conservation Committee.

Mitchell, P. I., Newton, S. P., Ratcliffe, N., & Dunn, T. E. (2004). *Seabird Populations of Britain and Ireland*. London: T & AD Poser.

Newton, I. (1998). *Population Limitation in Birds.* London: Academic Press.

Parrott, D. (2015). Impacts and management of common buzzards *Buteo buteo* at pheasant *Phasianus colchicus* release pens in the UK: a review. *European Journal of Wildlife Research, 61*, 181-197.

Ratcliffe, N. (2003). Little terns in Britain and Ireland: estimation and diagnosis of population trends. In R. I. Allcorn (Ed.), *Proceedings of a symposium on Little Terns Sterna albifrons* (pp. 4-18). Sandy, UK: RSPB Research Report No. 8.

Redpath, S. M., Thirgood, S. J., & Leckie, F. M. (2001). Does supplementary feeding reduce predation of red grouse by hen harriers? *Journal of Applied Ecology, 38*, 1157-1168.

Redpath, S. M., Young, J., Evely, A., Adams, W. M., Sutherland, W. J., Whitehouse, A., Amar, A., Lambert, R. A., Linnell, J. D. C., Watt, A., & Gutierrez, R. J. (2013). Understanding and managing conservation conflicts. *Trends in Ecology & Evolution, 28*, 100-109.

Roos, S., Smart, J., Wilson, J. D., & Gibbons, D. W. (2018). A review of predation as a limiting factor for UK bird populations in mesopredator-rich landscapes: the UK as a case study. *Biological Reviews*.

SAS Institute Inc. (2015). SAS/STAT 14.1 Users' Guide. In (Vol. 2017): Cary NC.

Smart, J. (2003). Managing colonies for Little Terns. In R. I. Allcorn (Ed.), *Proceedings of a symposium on Little Terns Sterna albifrons* (pp. 19-28). Sandy, UK: RSPB Research Report No. 8.

Smart, J., Amar, A., Sim, I. M. W., Etheridge, B., Cameron, D., Christie, G., & Wilson, J. D. (2010). Illegal killing slows population recovery of a re-introduced raptor of high conservation concern – the red kite *Milvus milvus*. *Biological Conservation, 143 (5)*, 1278-1286.

Smart, J., & Ratcliffe, N. (2000). Monitoring the effectiveness of supplementary feeding as a means of reducing kestrel predation on little terns. In. Sandy, UK: RSPB Research Report.

Smith, M. E., Linnell, J. D. C., Odden, J., & Swenson, J. E. (2000). Review of Methods to Reduce Livestock Depredation II. Aversive conditioning, deterrents and repellents. *Acta Agriculturae Scandinavica, Section A — Animal Science, 50*, 304-315.

Smith, R. K., Pullin, A. S., Stewart, G. B., & Sutherland, W. J. (2010). Effectiveness of predator removal for enhancing bird populations. *Conservation Biology, 24*, 820-829.

Smith, R. K., Pullin, A. S., Stewart, G. B., & Sutherland, W. J. (2011). Is nest predator exclusion an effective strategy for enhancing bird populations? *Biological Conservation, 144*, 1-10.

Storey, T. H. (1997). *Effects of diversionary feeding on raccoon foraging behaviour in southwestern Georgia.*, The University of Georgia.

Summers, R. W., Willi, J., & Selvidge, J. (2009). Capercaillie Tetrao urogallus Nest Loss and Attendance at Abernethy Forest, Scotland. *Wildlife Biology, 15*, 319-327.

Thompson, K. R., Brindley, E., & Heubeck, M. (1997). Seabird numbers and breeding success in Britain and Ireland, 1996. In (Vol. UK Nature Conservation no. 21). Peterborough: Joint Nature Conservation Committee.

Watson, M., Aebischer, N. J. & Cresswell, W. (2007). Vigilance and fitness in grey partridges *Perdix perdix*: the effects of group size and foraging-vigilance trade-offs on predation mortality. *Journal of Animal Ecolog*y, 76, 211-221.

Watson, M., Aebischer, N. J., Potts, G. R., & Ewald, J. A. (2007). The relative effects of raptor predation and shooting on overwinter mortality of grey partridges in the United Kingdom. *Journal of Applied Ecology, 44*, 972-982.

Wiehn, J., Ilmonen, P., Korpimaki, E., Pahkala, M., & Wiebe, K. L. (2000). Hatching asynchrony in the Eurasian kestrel Falco tinnunculus: an experimental test of the brood reduction hypothesis. *Journal of Animal Ecology, 69*, 85-95.

Figure captions

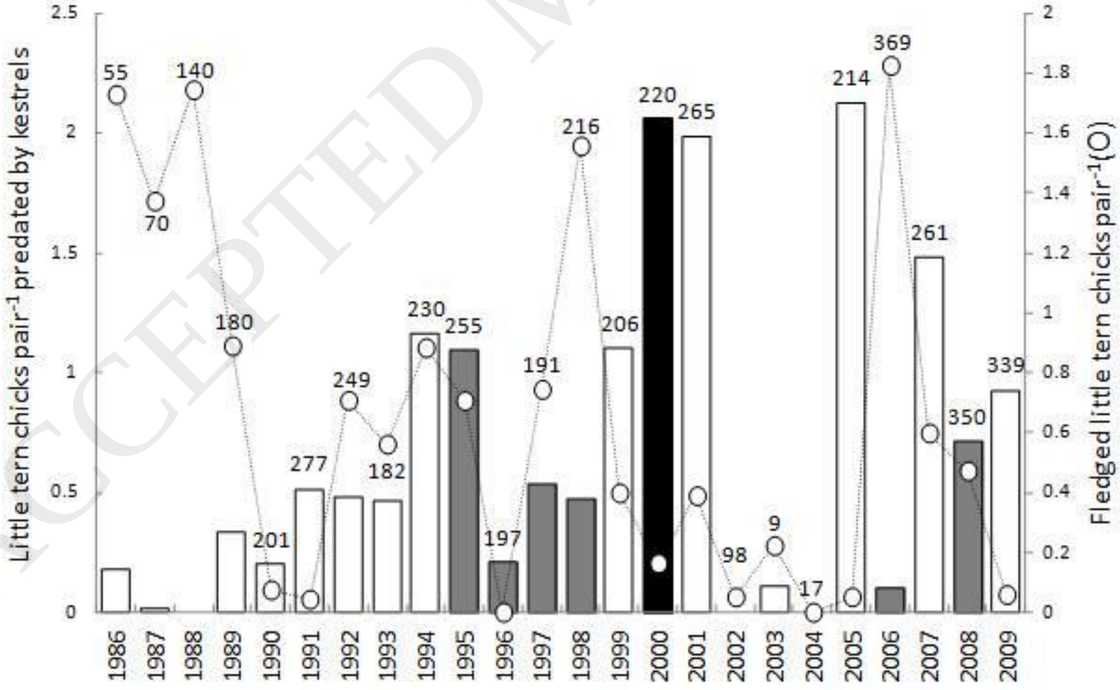
Figure 1. The number of nesting pairs and breeding success of little terns (pairs = numbers, chicks fledged pair^{-1} = open circles) and the predation pressure from kestrels (little tern chicks pair^{-1} predated by kestrels = bars) between 1986, the first year of protection by the RSPB and 2009, the last year that little terns nested at the colony. Shading of the bars indicates whether diversionary feeding was used all season (grey bars), part season (black bar) or not (white bars).

Figure 2. Map of Great Yarmouth and the surrounding area, showing the location of the little tern colony, the area searched for kestrel nests and the location of the focal kestrel nests (2006-2009) in each year during the formal experiment. Inset shows the location within the UK.

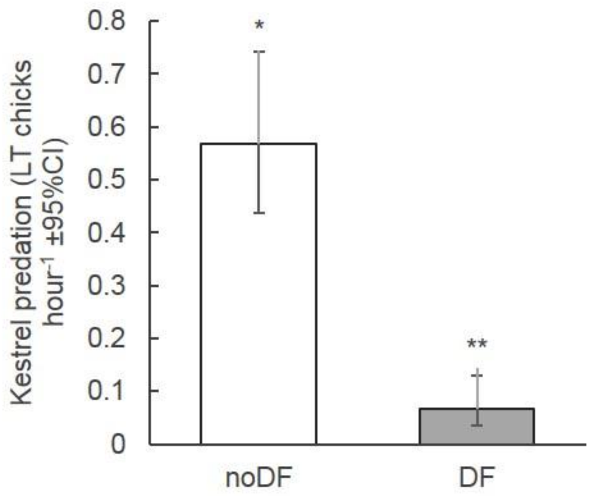
Figure 3. The mean hourly rate of predation of little terns chicks by kestrels during timed watches (2006-09) in relation to years with DF (grey bars) and without DF (white bars). Different numbers of asterisks denote significant differences between bars (P < 0.001). See table 1 for statistical tests.

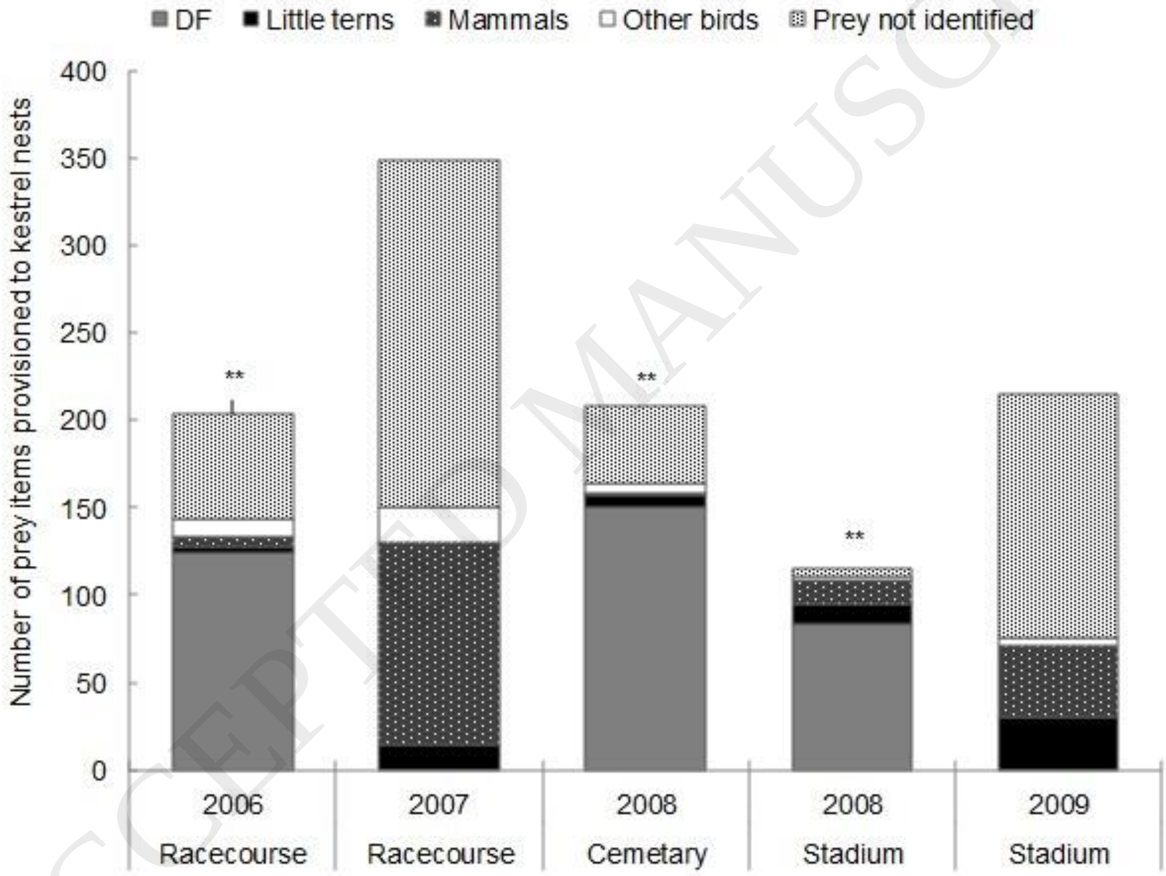
Figure 4. The number of different prey items observed being provisioned to different kestrel nests between 2006 and 2009, using nest cameras supplemented by timed observations. Prey type is split into DF (diversionary food: grey), little terns (black), mammals (dark grey spotted), other birds (white) and prey not identified (light grey spotted). Years with DF are denoted by **.

Figure 5. The mean (± 95%CIs) number of wild prey items day^{-1} (white bars) and little tern chicks day^{-1} (grey bars) provisioned at monitored kestrel nests in relation to diversionary feeding. Nests were monitored using nest cameras supplemented by timed observations. For wild prey and little tern chicks separately, different numbers of asterisks denote significant differences (P < 0.001). See table 1 for the statistical tests.



© OpenStreetMap (and) contributors, CC-BY-SA, Sources: Esri, DeLorme, USGS, NPS


Kestrel predation (LT chicks hour⁻¹ ±95%CI)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
*
**
noDF
DF


▨ DF
■ Little terns
▩ Mammals
☐ Other birds
▦ Prey not identified
Number of prey items provisioned to kestrel nests
400
350
300
250
200
150
100
50
0
**
**
**
2006 Racecourse
2007 Racecourse
2008 Cemetary
2008 Stadium
2009 Stadium

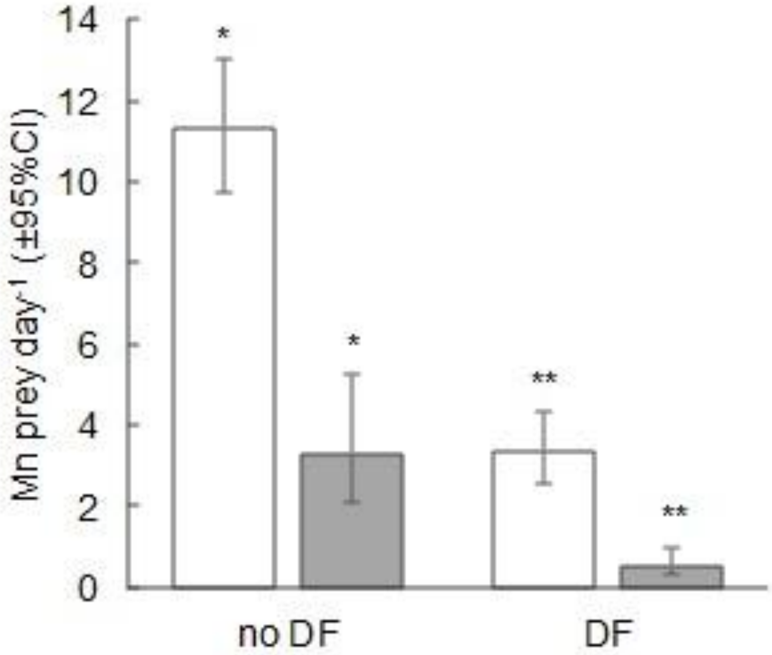

Mn prey day⁻¹ (±95%CI)
14
12
10
8
6
4
2
0
*
*
**
**
no DF
DF

Table 1. Results of GLMs to assess the effects of diversionary feeding on kestrel predation at the little tern colony and prey provisioning at monitored kestrel nests. Significant effects retained in final models are in bold with statistics from the final models. Non-significant effects not retained in final models are in italics with statistics from the full models. *Statistics are taken from the zero inflation model when explicitly modelling the excess zeros and OTHER WILD PREY includes wild mammals and birds other than little terns.

Response variable	Fixed effects	F	Num, Den DF	P
Question 2: Was kestrel predation at the little tern colony lower when focal kestrel nests were fed diversionary food?				
Kestrel predation rates	**DF**	**41.7**	**1,134**	**<0.0001**
(Fig. 3)	**Colony size**	**5.5**	**1,134**	**0.02**
	SEASON DAY	**12.7**	**1,134**	**0.0005**
	SEASON DAY^2	**13.4**	**1,134**	**0.0004**
Question 3: Was provisioning of little tern and other wild prey at kestrel nests reduced when they were fed diversionary food?				
Provisioning - all wild prey	**DF**	**74.1**	**1,99**	**<0.0001**
(Fig. 5)	*Colony size*	*4.34*	*1,96*	*0.04*
	SEASON DAY	*0.02*	*1,96*	*0.9*
	SEASON DAY^2	*0.5*	*1,96*	*0.48*
		Chi-sq	DF	P
Provisioning - little tern prey	**DF**	**14.6**	**1,95**	**0.0001**
(Fig. 5)	**SEASON DAY**	**4.5**	**1,95**	**0.03**
	SEASON DAY^2	**8.2**	**1,95**	**0.004**
	***OTHER WILD PREY**	**13.5**	**1,95**	**0.0003**
	Colony size	*0.38*	*1,93*	*0.53*