Fearing the feline: domestic cats reduce avian fecundity through trait-mediated indirect effects that increase nest predation by other species

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Summary

1. Urban areas contain high densities of non-native species, which in the UK include the domestic cat *Felis catus* (Linnaeus 1758) and the grey squirrel *Sciurus carolinensis* (Gmelin 1788). The direct predation effects of domestic cats on prey populations attract intense debate, and such influences of the nest-predatory grey squirrel are receiving increasing attention. In contrast, theory predicts that sublethal and indirect effects are more important, but empirical evidence is currently lacking.

2. We conducted controlled model presentation experiments at active urban blackbird *Turdus merula* (Linnaeus 1758) nests to provide the first empirical evidence that quantifies the potential sublethal and indirect effects of predators (domestic cat and grey squirrel) on avian reproductive success.

3. Domestic cat models reduced subsequent parental provisioning rates, a strong indicator of sublethal effects, by one-third relative to a nonpredatory rabbit *Oryctolagus cuniculus* (Linnaeus 1758) control. There was no compensatory increase in food load size. Previous experiments demonstrate that this magnitude of reduced food delivery will reduce nestling growth rates by *c.* 40%. The grey squirrel model induced similar but weaker effects.

4. Following the brief presence of the domestic cat model, subsequent daily nest predation rates, chiefly by corvids, increased by an order of magnitude relative to the squirrel and rabbit models. The intensity of parental nest defence elicited in response to model presentations predicts the probability of such third-party predator predation events, and the domestic cat model generated significant increases in nest defence behaviour.

5. *Synthesis and applications.* The brief presence of a domestic cat at avian nest sites reduces subsequent provisioning rates and induces lethal trait-mediated indirect effects. We provide the first robust evidence for these latter effects in any avian predator–prey system, although they are likely to be common in many avian assemblages with high predator densities. It is imperative that future assessments of the impact of predatory species on avian prey species take lethal trait-mediated indirect effects into account, as so doing will prevent biased estimates of predator effects and facilitate the design of more effective control strategies. Full mitigation of the sublethal and indirect effects of domestic cats would problematically require permanent indoor housing.

Key-words: chick growth rate, crows, eavesdropping, gray squirrel, nest defence, non-native species, provisioning rate, Skutch's hypothesis, songbirds, urbanisation

Introduction

The non-native domestic cat *Felis catus* (Linnaeus 1758) is one of the commonest avian predators in urban areas with typical densities in some regions of approximately 400 cats per km^2, although they can exceed 1500 per km^2 (Sims *et al.* 2008). Domestic cats are frequently considered a major predator of adult birds and nestlings. They contribute significantly to mortality in local avian populations and kill up to 29 million birds per year in Britain, yet their full impacts on avian populations remain

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controversial and unresolved (Churcher & Lawton 1987; Woods, McDonald & Harris 2003; Baker *et al.* 2008; Sims *et al.* 2008; van Heezik *et al.* 2010). One major reason for this uncertainty is the lack of empirical studies assessing the potential for domestic cats to influence avian populations through sublethal effects (Beckerman, Boots & Gaston 2007).

Predators influence prey populations through direct consumption, that is, lethal effects, and indirectly through prey species altering their behaviour to minimize predation risk in a manner that reduces population growth rates (Lima 1998). These behavioural modifications are termed sublethal effects and may have considerable implications for population and community dynamics of prey species (Agrawal 2001). Theory and modelling studies suggest that the impacts of sublethal effects on avian prey populations are frequently greater than those arising from lethal effects, but empirical evidence is very limited (Cresswell 2008, 2011). Skutch's hypothesis describes one mechanism through which nest predators can impose sublethal effects on bird populations. It proposes that birds respond to increased nest predation risk by reducing the rate at which offspring are provisioned, thus promoting smaller clutches unless there is a compensatory increase in the amount of food delivered per trip (Skutch 1949). Reduced nestling provisioning in response to nest predators can also reduce nestling growth rates and condition (Dunn, Hamer & Benton 2010). A small number of intraspecific studies provide empirical evidence for reduced provisioning rates in response to nest predators (Ghalambor & Martin 2000; Dunn, Hamer & Benton 2010) that can promote smaller clutches (Zanette *et al.* 2011). In contrast, other studies find no evidence that nest predator presence reduces provisioning rates (Tilgar, Moks & Saag 2011). We are not aware of any empirical studies assessing provisioning rates in response to domestic cats or any other sublethal effects of this predator, but modelling studies predict these to be high (Beckerman, Boots & Gaston 2007).

In addition to their sublethal effects, predators can determine prey population growth rates through other indirect mechanisms by altering prey species' traits in a manner that changes their interactions with other species (Abrams 2007). Theory and an emerging body of empirical research suggest that such trait-mediated indirect effects can have large effects on prey populations (Abrams 2007; Peckarsky *et al.* 2008; Duffy *et al.* 2011). Increased nest predation risk changes parental behavioural traits by eliciting aggressive nest defence behaviour. This frequently reduces the rate of nest predation by the focal predator (Klump & Shalter 1984; Montgomerie & Weatherhead 1988; Fallow & Magrath 2010). This defence behaviour could impose a cost by attracting additional predators to the nest site, thus increasing subsequent nest predation rates and generating a lethal trait-mediated indirect effect. This hypothesis has received very limited attention, and its validity remains uncertain. The few experimental tests

that have been conducted, while useful, provide insufficient support as they relied on playing recordings of avian mobbing calls at artificial nests in nest boxes (Krama & Krams 2005; Krams *et al.* 2007). These studies thus ignore the specific identity of the focal predator, the potential that parental birds reduce the use of vocalizations during nest defence in the presence of predators that use vocalizations to locate nests, and the influence of parental nest defence on subsequent nest predation rates. Indeed, parents that engage in nest defence that is sufficiently vigorous to attract additional predators may be capable of conducting an effective defence against such predators. Taking parental responses to predators, such as nest defence, into account is widely considered essential for accurate assessment of predator impacts and associated predation risk (Cresswell 1997; King *et al.* 1999).

Here, we assess the hypotheses that the presence of domestic cats reduces the rate at which urban birds provision their young, creating the potential for sublethal effects, and induces lethal trait-mediated indirect effects by increasing the rates of nest predation by other species. We do so using the blackbird *Turdus merula* (Linnaeus 1758) as a case study. This is one of the commonest European urban birds and provides an ideal case study as it is emerging as a model species for assessing the impacts of urban development (Partecke, Schwabl & Gwinner 2005; Evans *et al.* 2009); exhibits defensive behaviour towards potential predators (Dabelsteen & Pederson 1990); and breeding success is not adversely influenced by human visitation to the nest (Ibáñez-Álamo & Soler 2010). We use an experimental model presentation approach in which models are presented for 15 min and then removed, and avian responses are recording during and after model presentation. We compare blackbirds' responses to domestic cats with a non-predatory control species (rabbit *Oryctolagus cuniculus*; Linnaeus 1758) and an additional non-native mammalian nest predator, the grey squirrel *Sciurus carolinensis* (Gmelin 1788) that is common in urban areas (Parker & Nilon 2008). We selected the latter species as there is anecdotal evidence that it may regulate avian population size through nest predation (Hewson *et al.* 2004), and more rigorous analyses suggest that these effects may limit the population size of a small number of species, including blackbirds (Newson *et al.* 2010a,b) but the potential sublethal effects of grey squirrels have not yet been quantified.

Materials and methods

MODEL PRESENTATION AND RECORDING BEHAVIOURAL RESPONSES

Blackbird nests were located during the 2010 and 2011 breeding seasons (March to August) within urban Sheffield, England (53° 22′N, 1°20′W); this is the fifth largest urban area in the UK and contains *c.* 555 500 people (Office for National Statistics 2010). Urban areas were defined, following previous work in this region

(Gaston *et al.* 2005), as 1 × 1 km squares with at least 25% coverage of hard surface. Blackbird nests were found by searching suitable nest sites (primarily scrub, bushes and small trees) and by using parental behavioural cues.

In 2010, we used taxidermy mounts of an adult domestic cat (tabby colouration), an adult grey squirrel, and an adult rabbit (natural grey morph) as a non-predator control. All model species occur within the study region. In 2011, we used one additional model of each species, taxidermy mounts of an adult squirrel and rabbit (grey morph), and a replica adult domestic cat (black and white morph). Model presentations typically commenced the day following nest discovery or, in one quarter of cases, 1·5 h after the nest finder left the nest site to enable parents to resume normal behaviour. Model presentations were conducted at the (i) egg, (ii) young chick rearing (1–4 days), and (iii) old chick rearing (8 days or older) stages using hatch date or morphological criteria to determine chick age (Mayer-Gross 1970). Different sets of nests were used for each of these three stages. Within each stage, each nest was exposed to all three model species in a randomized order of presentation over a 3-day period, with each presentation being 24 h apart. All nests remained within this focal stage during this 3-day period. In 2011, when two model types were available for each species the focal model type was selected at random.

Presentations were only conducted during dry conditions with light winds (<4 on the Beaufort scale). Models were placed on the ground, approximately 2 m away from, and facing, the blackbird's nest. Average nest height was $1·25 ± 0·068$ m (range 0·25–2 m, $n = 68$). Models were left out for 15 min and then removed. Fifteen minutes was considered an optimal period. It provides sufficient time for parent birds to notice the model, and it is within the time range during which mammalian predators typically remain within the vicinity of birds' nests (Schaefer 2004) but limits the probability of habituation to a stationary model. During the presentation period, parental behaviour was recorded from a concealed location 15–30 m away from the nest. We recorded the number of 3-min periods during which parental blackbirds alarm called. Aggressive behaviour was recorded as the sum of the number of occasions on which an adult blackbird reacted to the model by striking, diving towards or hovering within 2 m of it. All scores were summed across the male and female to give an overall metric of parental defence. These protocols follow the procedures outlined in Knight & Temple (1988) who similarly assessed defensive behaviour of nesting birds to model predators. Each focal nest was at least 100 m away from the nearest other blackbird nest and only one male and one female were observed responding to the models; we thus assume that all observations concern the social parents of the focal nest.

After this 15-min period, the model was removed and provisioning visits were observed and then provisioning rates (h^{-1}) were calculated. Across the survey seasons, provisioning watches were between 45 and 60 min duration (mean duration and standard errors at the young chick stage $56·00 ± 1·23$ min, $n = 30$; old chick stage $55·86 ± 1·27$ min, $n = 29$). In 2011, food load size was also recorded using a miniature digital camera (Mini DV Camera, Thumbs Up (UK) Ltd, Ruislip, UK). The number of food items brought to the nest was recorded and the size of each item was estimated in relation to parent beak length in 0·25 intervals (range 0·25–2·25 of beak length). Load size was calculated by summing the lengths of each food item within a load. In 2011, the duration of provisioning watches was extended to 90 min at nine nests with young chicks and seven nests with old chicks.

This 90-min period was split into two 45-min sections, and the number of visits made to the nest by parent birds in each was recorded to assess whether parental provisioning rates increased with the amount of time that elapsed following exposure to the model. This was only assessed for the cat as this model consistently had a significant influence on avian provisioning activity.

To quantify lethal trait-mediated effects, we recorded the fate (predated or not predated) of each nest 24 hours after the presentation of each model. We focus on this time period as after 24 hours the nest was exposed to a different model species. Nests were recorded as predated if contents were missing, and offspring were too young to fledge, or egg shell fragments or chick remains were present in or close to the nest. Avian and mammalian predators were distinguished by a combination of signs including beak, bite and scrape marks on offspring, the presence of predator droppings and whether the nest was left intact or damaged; damaged nests indicating mammalian predation (Davison & Bollinger 2000; Lyver 2000; Currie *et al.* 2005; Mason, Desmond & Agudelo 2005).

STATISTICAL ANALYSES

Analyses were conducted using R software v. 2.9.2 (2009; R Foundation for Statistical Computing, Vienna, Austria) Parental alarm calling, aggression and provisioning rates were analysed separately for nests from 2010 and 2011, and for each of the three stages. Each analysis was only conducted for nests that had been exposed to all three model species. In 2010, data were available at the egg, young chick and old chick stages from, respectively, 17, 15 and 15 nests; in 2011 equivalent figures were 20, 15 and 14. Sample sizes varied between stages as a consequence of nest failure, and some nests were also discovered after incubation. Alarm calling rates, aggressive behaviour and food load size were not normally distributed (Shapiro–Wilk test: $P < 0·05$). We thus used the nonparametric Friedman's test to assess how these variables were associated with the models' specific identity; when overall significant differences were detected we used Wilcoxon signed-rank *post hoc* tests, these *post hoc* tests are not automatically adjusted for multiple testing so this was achieved using Bonferroni adjustments.

Provisioning rates were normally distributed (data for provisioning rates to older chicks in 2011 were $\log_{10}$ transformed to meet the normality assumption; Shapiro–Wilk test: $P > 0·05$ in all cases) and we thus used a repeated measures ANOVA to assess how provisioning rates varied in response to the models' specific identity. Levene's test indicated that samples had equal variance and we thus used Tukey's *post hoc* comparison tests (which automatically corrects for experiment-wise error rate when there are multiple comparisons being made, by providing adjusted *P* values: Maxwell & Delaney 2004). In 2011, two different forms of each model species were used, but avian responses to the two versions of each model species did not exhibit significant differences (see Table S1, Supporting Information), and we thus pooled data within model species. Variation in chick provisioning rates in the two focal 45-min periods used in 2011 was analysed using the nonparametric Wilcoxon matched pairs test.

Two analyses were conducted to test the lethal trait-mediated indirect effect hypothesis, and these used all nests that were exposed to at least one model species. First, we assessed if model species identity was associated with nest predation rates within the 24 h period following exposure to the model. These analyses used data pooled across years and were only conducted at the egg and

young chick stages, as no such predation events were recorded at the old chick stage, presumably because at this stage nestlings are sufficiently well developed to disperse rapidly from the nest site when an approaching predator is detected (Snow 1958). Data were available at the egg stage for 39, 42 and 43 nests exposed, respectively, to the rabbit, grey squirrel and domestic cat models; equivalent sample sizes for the young chick stage were 30, 30 and 32. Data were analysed using Fisher's exact test. Finally, we tested the prediction derived from the lethal trait-mediated indirect effect hypothesis that nests at which parents exhibited higher alarm calling rates and more aggressive behaviour had a higher probability of being predated. We pooled data across years and constructed logistic regression models (using LME4 package Comprehensive R Archive Network, http://cran.r-project.org/web/packages/lme4/lme4.pdf) of nest fate (i.e. predated or not predated) and used parental alarm calling rate, aggressive behaviour, year (as a fixed factor) and nest identity (as a random factor) as predictors. Model species was not included as a predictor as this is strongly associated with parental behaviour and would have introduced strong collinearity into the model. Model selection adopted an information theoretic approach; all models contained nest identity and we constructed all possible models given the suite of our other predictor variables. We used Akaike Information Criteria (AICc to correct for small sample sizes) to calculate each model's weight, that is, the probability that it provides the most parsimonious fit to the data. The smallest number of models whose cumulative weights summed to 0·95 was included in the 95% confidence set of models, and model averaging was conducted across this set of models to assess the influence of alarm calling rate and aggressive behaviour on nest fate.

Results

PARENTAL RESPONSES

The domestic cat model consistently elicited significantly higher alarm calling rates, by an order of magnitude, than the control rabbit, and alarm calling was also increased relative to the grey squirrel, with these differences significant at most offspring stages (Table 1; Figs 1a,b and S1, Supporting Information). Alarm calling rates tended to be higher in response to the grey squirrel than the rabbit, but these differences were only significant during the incubation stage in 2010 (Table 1; Figs 1a,b and S1, Supporting Information). Direct aggression towards the model did not vary with model identity during incubation. At the young chick stage aggression was higher in response to the domestic cat than the squirrel or rabbit, but differences were not significant (Table 1; Figs 1c,d and S1, Supporting Information). When old chicks were in the nest, aggression towards the domestic cat was significantly higher, by an order of magnitude, than towards the rabbit and grey squirrel (Table 1; Figs 1c,d and S1, Supporting Information). Aggression also tended to be higher towards the squirrel than the rabbit, but these differences were not significant (Table 1; Figs 1c,d and S1, Supporting Information).

Following exposure to the domestic cat model, and its subsequent removal, parental blackbirds reduced their provisioning rates by over one-third relative to the rabbit

control, and rates were also typically significantly reduced relative to the grey squirrel (Table 1; Fig. 2). There was no evidence that provisioning rates returned to normal 90 min after removal of the domestic cat model (Table 2). Provisioning rates tended to be lower following presentation of the squirrel relative to presentation of the rabbit, but these differences were only significant at the old chick stage in 2010 (Table 1; Fig. 2). Food load size was not recorded in 2010, but in 2011 did not vary with model type at either the young (Friedman's test: $\chi^2 = 0.41$; $P > 0.05$) or old chick stage ($\chi^2 = 4.50$; $P > 0.05$; Figs 3 and S2, Supporting Information).

PREDATION RATES

Of the 16 nests that were predated following exposure to a model 44% were predated by birds, 19% by mammals, and 37% were predated by an unidentified predator. Pooling results across the survey years, predation rates of blackbird nests during incubation and within 24 hours of model exposure varied significantly in response to model species identity ($P < 0.001$). Predation rates were higher following exposure to the domestic cat (23%, $n = 43$) than the rabbit (0%, $n = 39$; $P < 0.01$) and the grey squirrel (5%, $n = 42$; $P < 0.05$), and were not significantly higher following exposure to the grey squirrel than the rabbit ($P > 0.05$). During the young chick rearing period, predation rates of the nests within 24 hours of model exposure varied significantly in response to presentation of the three model species ($P = 0.032$), with all of this predation occurring in response to the cat model (13%, $n = 32$ nests), with no nests exposed to the grey squirrel ($n = 30$) or rabbit ($n = 30$) being predated. No predation event was recorded within 24 hours of model exposure during the old chick rearing period, presumably because at this stage nestlings are sufficiently well developed to disperse rapidly from the nest site when threatened by a predator (Snow 1958).

Logistical models of nest fate demonstrated that the probability of nest predation within 24 hours of model exposure increased with the amount of parental nest defence. During the incubation stage, nest predation rates increased with parental alarm calling behaviour (model averaged partial $D^2 = 0.34$; Table 3), and parental aggression levels had a negligible effect on predation probability (model averaged partial $D^2 = 0.01$; Table 3). At the young chick stage, the probability of nest predation increased with both alarm calling rates (model averaged partial $D^2 = 0.12$; Table 3) and parental aggression levels (model averaged $D^2 = 0.08$; Table 3).

Discussion

When domestic cats were close to urban blackbird nests, there was a consistent and significant increase in parental alarm calling rates, relative to the nonpredatory rabbit control. The domestic cat also elicited significantly higher levels of direct aggression when old chicks were in the

Table 1. Differences in parental urban blackbird alarm, aggression and provisioning rates in response to presentation of three model species the predatory domestic cat and grey squirrel, and the nonpredatory control rabbit

Response	Nest stage	Year	Overall comparison	Post hoc testing		
				Cat vs. rabbit	Cat vs. squirrel	Squirrel vs. rabbit
Alarm	Incubation	2010	χ^2 = **10.53; P = 0.0052**	C > R; Z = −2.34; P = 0.019	C > S; Z = −1.47; P = 0.140	S > **R; Z = −2.59; P = 0.010**
		2011	χ^2 = **14.86; P = 0.0006**	C > **R; Z = −2.95; P = 0.003**	C > **S; Z = −2.49; P = 0.013**	S > R; Z = −2.23; P = 0.026
	Young chick	2010	χ^2 = **15.14; P = 0.0005**	C > **R; Z = −2.91; P = 0.004**	C > **S; Z = −2.94; P = 0.003**	S > R; Z = −0.56; P = 0.573
		2011	χ^2 = **9.56; P = 0.0084**	C > **R; Z = −2.76; P = 0.006**	C > S; Z = −1.75; P = 0.081	S > R; Z = −1.98; P = 0.048
	Old chick	2010	χ^2 = **16.12; P = 0.0003**	C > **R; Z = −3.08; P = 0.002**	C > **S; Z = −3.18; P = 0.001**	S > R; Z = −1.43; P = 0.153
		2011	χ^2 = **17.24; P = 0.0002**	C > **R; Z = −3.08; P = 0.002**	C > **S; Z = −3.02; P = 0.003**	S > R; Z = −1.50; P = 0.135
Aggression	Incubation	2010	χ^2 = 3.50; P = 0.1738	n/a	n/a	n/a
		2011	χ^2 = 4.00; P = 0.1353	n/a	n/a	n/a
	Young chick	2010	χ^2 = **8.32; P = 0.0156**	C > R; Z = −2.27; P = 0.023	C > S; Z = −1.95; P = 0.052	S > R; Z = −1.00; P = 0.317
		2011	χ^2 = 5.14; P = 0.0764	n/a	n/a	n/a
	Old chick	2010	χ^2 = **17.43; P = 0.0002**	C > **R; Z = −2.68; P = 0.007**	C > **S; Z = −2.68; P = 0.007**	S > R; Z = −1.00; P = 0.317
		2011	χ^2 = **15.93; P = 0.0003**	C > **R; Z = −2.69; P = 0.007**	C > **S; Z = −2.54; P = 0.011**	S > R; Z = −1.34; P = 0.180
Provisioning rate	Young chick	2010	$F_{2,28}$ = **9.23; P = 0.0008**	C < **R; Q = 5.94, P = 0.001**	C < **S; Q = 4.06; P = 0.020**	S < R; Q = 1.89; P = 0.389
		2011	$F_{2,28}$ = **3.48; P = 0.0447**	C < **R; Q = 3.60, P = 0.043**	C < S; Q = 2.66; P = 0.163	S < R; Q = 0.94; P = 0.679
	Old chick	2010	$F_{2,28}$ = **12.67; P = 0.0001**	C < **R; Q = 7.12, P = 0.0001**	C < **S; Q = 3.56; P = 0.046**	S < **R; Q = 3.56; P = 0.046**
		2011	$F_{2,26}$ = **6.10; P = 0.0067**	C < **R; Q = 3.97, P = 0.031**	C < **S; Q = 4.53; P = 0.004**	S > R; Q = 0.55; P = 0.935

Overall comparisons of provisioning rate are assessed using one way ANOVAs followed by Tukey's *post hoc* tests that correct for multiple comparisons. Significant differences are in bold. All other overall comparisons were conducted using the nonparametric Friedman's test, followed by Wilcoxon signed-rank *post hoc* tests. The latter do not automatically correct for multiple comparisons so Bonferroni adjustments were conducted when interpreting significance levels and thus only *post hoc* tests with $P < 0.017$ are considered significant (in bold); results that were significant prior to Bonferroni adjustments but not subsequently are in italics
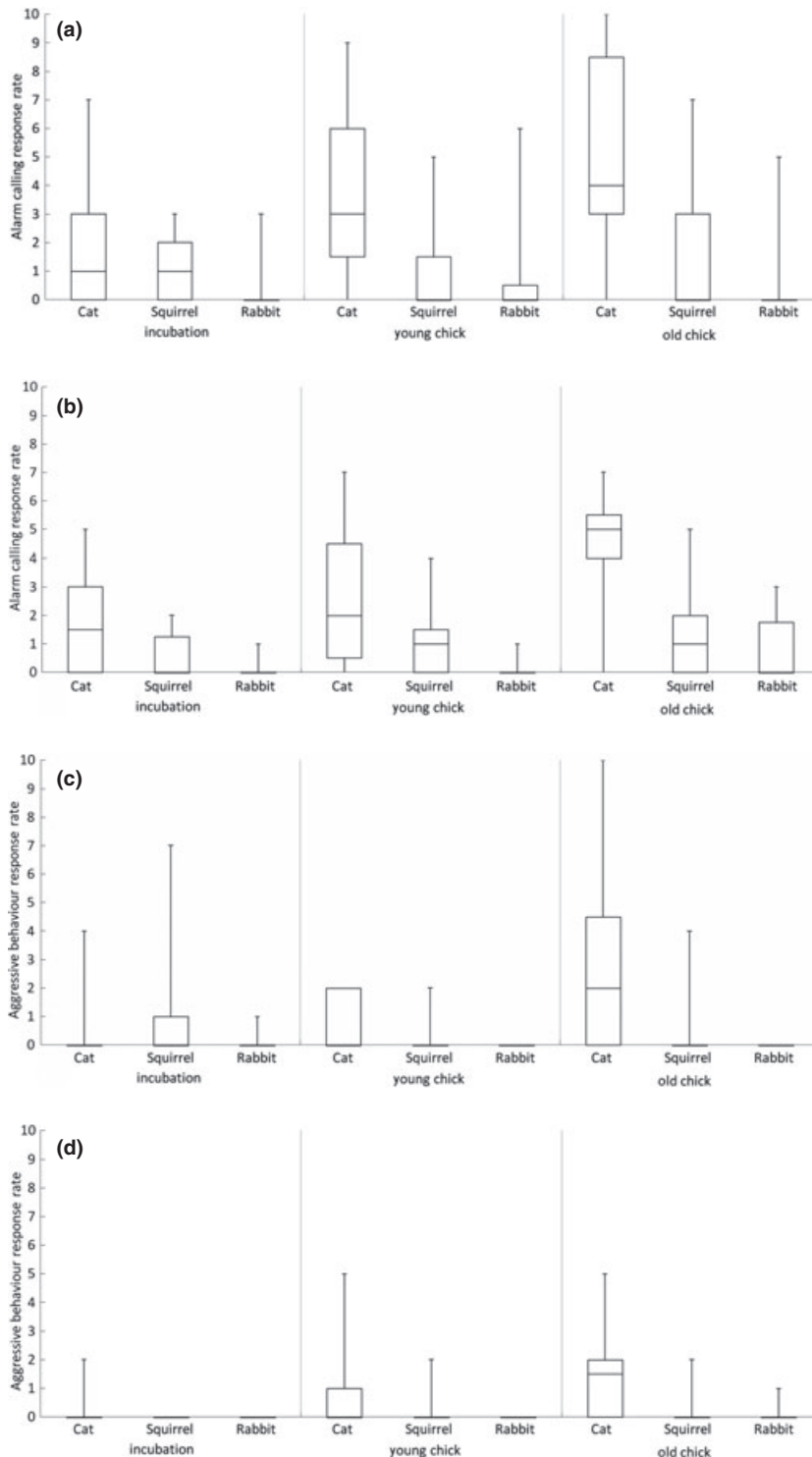
Fig. 1. Box and whisker plots of parent blackbird alarm calling rates in (a) 2010 and (b) 2011, and parent aggressive behaviour in (c) 2010 and (d) 2011 in response to presentation of a domestic cat, grey squirrel and rabbit control model close to active nests, at three nesting stages. The three horizontal lines in the boxes represent the 25% quartile, the median and the 75% quartile; in some cases one or more of these values are identical and thus fewer than three lines are shown. The whiskers represent minimum and maximum values and are only presented when they differ from the 25% and 75% quartiles respectively.

nest. The increased aggression at the old chick stage, relative to younger offspring, supports parental investment theory, which predicts that parents should invest more heavily in older rather than younger offspring to maximize their fitness (Dawkins & Carlisle 1976). Parental blackbirds exhibited comparable but much weaker responses to the grey squirrel model. Consequently, while both the domestic cat and grey squirrel are recognized as predators, generating the potential for sublethal effects,

the grey squirrel is perceived as much less of a threat than the domestic cat. This is probably partly because domestic cats can also predate adult birds, while grey squirrels are exclusively nest predators, but the situation may also arise because grey squirrels predate nests less regularly than domestic cats.

Following exposure to the domestic cat model, parental blackbirds significantly reduced provisioning rates by more than one-third; provisioning rates remained at this
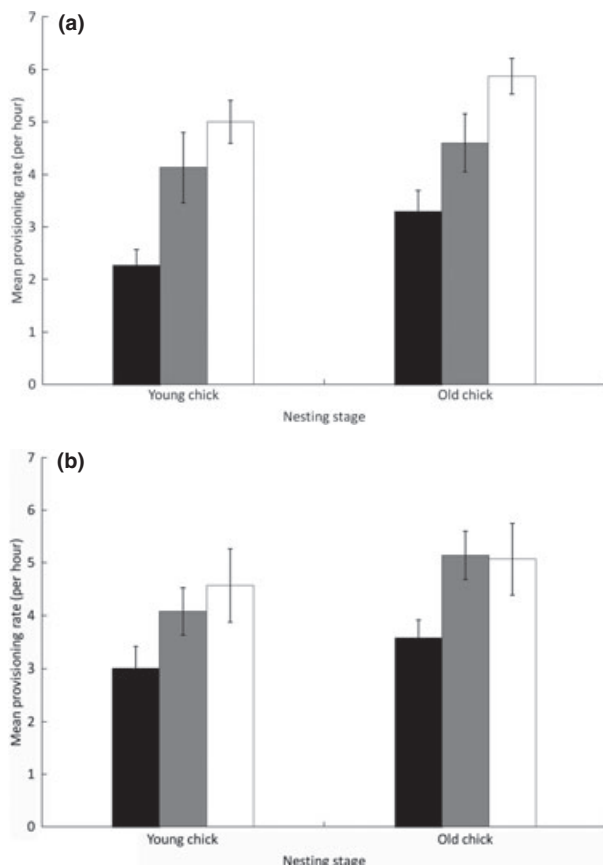
Fig. 2. Parental blackbird mean hourly provisioning rates following exposure, and subsequent removal, of a domestic cat (black bar), grey squirrel (grey bar) and rabbit control (white bar) model during three nesting stages in (a) 2010 and (b) 2011. Error bars represent standard errors.

level for at least 90 minutes following removal of the cat model. Moreover, there was no compensatory increase in the amount of food delivered, which contrasts with the theory that breeding birds can compensate for reduced provisioning rates by increasing the amount of food delivered per trip to the nest (Skutch 1949; Martin *et al.* 2000). Reduced food delivery, even over short time periods, can adversely influence chick condition and reproductive success (Schwagmeyer & Mock 2008; Dunn, Hamer & Benton 2010; Martin *et al.* 2011), and over longer time periods can promote smaller clutches (Skutch 1949; Martin *et al.* 2000). Our results provide the first empirical evidence that domestic cats have the potential

to exert such effects. We do not know if such sublethal effects arise in our focal urban blackbird populations, but they seem highly likely to occur as experimental studies indicate that nestling growth rates in *Turdus* species are reduced by approximately 40% when food intake rates are reduced by one-third of the normal rate (Konarzewski & Starck 2000). It thus seems highly plausible that the high densities of domestic cats in urban areas (Sims *et al.* 2008) will generate sublethal effects that could contribute to the reduced chick condition and smaller clutch sizes that characterize urban bird populations in comparison with their rural conspecifics (Chamberlain *et al.* 2009), and contribute to their distinctive structure by reducing the abundance of species vulnerable to predation (Evans *et al.* 2011). The presence of grey squirrels also reduced provisioning rates under some circumstances. This indicates that grey squirrels could have the potential to influence avian reproduction through sublethal effects, but this potential is much more limited than is the case for the domestic cat.

During the incubation and chick rearing stages, the presence of the domestic cat model close to an active blackbird nest for just 15 minutes increased the probability of the nest being predated during the following 24 hours by an order of magnitude. The probability of nest predation during the incubation and chick rearing stages increased with the level of parental alarm calling during model exposure. The majority of this nest predation was conducted by birds, and corvids comprise over 99% of the avian nest predators in the study region (Fuller, Tratalos & Gaston 2008). We have thus demonstrated that the brief presence of a domestic cat close to an urban blackbird nest significantly increases parental alarm calling rates, and that these increased alarm calling rates are significantly associated with increased rates of nest predation by additional third-party predators. This appears to be the first robust empirical evidence for such lethal trait-mediated indirect effects in any avian predator-prey system that takes parental nest defence into account. These data thus indicate that the presence of domestic cats can significantly reduce avian breeding success by indirectly increasing nest predation rates. The most parsimonious mechanism for our findings is that alarm calling by parents attracts additional predators to the nest site. In addition, significant investment in nest defence may reduce parental ability to mount a successful nest defence against subsequent nest predators due to reduced energy reserves,

Table 2. Blackbird chick provisioning rates (h^{-1}) did not increase significantly between two 45 min recording periods following exposure to the domestic cat model, and remained significantly lower than equivalent control rates following exposure to the rabbit model

|	First period provisioning rate (±SE)	Second period provisioning rate (±SE)	Wilcoxon matched pairs test statistic cf. the two periods	Provisioning rate following exposure to the control model	Wilcoxon matched pairs test statistic cf. the second period and rabbit control
Young chick	2·89 ± 0·68 (n = 9)	3·11 ± 0·51 (n = 9)	V = 9·00; P > 0·05	4·86 ± 0·49 (n = 30)	V = 2·00; P < 0·05
Old chick	3·43 ± 0·75 (n = 7)	3·86 ± 0·55 (n = 7)	V = 3·00; P > 0·05	5·48 ± 0·37 (n = 29)	V = 1·50; P < 0·05
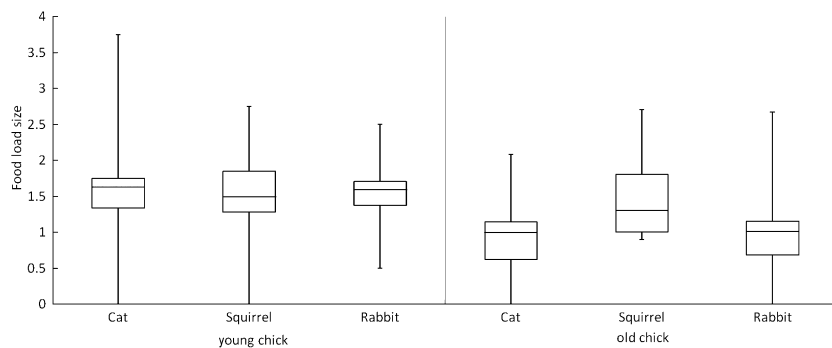
Fig. 3. Box and whisker plots of food load size during parental provisioning to young and old chicks following exposure, and subsequent removal, of a domestic cat, grey squirrel and rabbit control model in 2011. The three horizontal lines in the boxes represent the 25% quartile, the median and the 75% quartile. The whiskers represent minimum and maximum values.

Table 3. Results of logistic mixed models of nest fate (predated or not predated) in relation to parental alarm and aggression levels to model presentation. Nest is forced into all models and treated as a random factor; year is modelled as a fixed factor. Model selection follows an information theoretical approach and all models within the 95% confidence set are presented; model averaging is conducted over this set of models

Nest stage	Model	AICc	Model weight	Model D^2	Alarm (slope ± SE)	Alarm partial D^2	Aggression (slope ± SE)	Aggression partial D^2
Incubation	Alarm year nest	57·09	0·451	0·392	0·885 ± 0·230	0·316	0·000	0·000
	Alarm nest	58·64	0·208	0·342	0·954 ± 0·233	0·342	0·000	0·000
	Alarm aggression year nest	58·71	0·201	0·403	0·850 ± 0·225	0·389	0·267 ± 0·261	0·012
	Alarm aggression nest	59·43	0·140	0·362	0·827 ± 0·199	0·314	0·349 ± 0·253	0·020
	Model average	–	–	0·380	0·884 ± 0·229	0·336	0·102 ± 0·179	0·005
Young chick	Alarm aggression nest	40·64	0·340	0·305	1·314 ± 1·593	0·090	2·601 ± 2·392	0·079
	Alarm nest	41·07	0·274	0·226	1·067 ± 0·806	0·226	0·000	0·000
	Aggression nest	42·18	0·157	0·215	0·000	0·000	2·244 ± 1·438	0·215
	Alarm aggression year nest	42·59	0·128	0·322	1·400 ± 1·789	0·102	2·995 ± 3·182	0·088
	Alarm year nest	44·20	0·057	0·229	1·088 ± 0·830	0·228	0·000	0·000
	Model average	–	–	0·265	1·025 ± 1·269	0·124	1·694 ± 2·207	0·075

or because parents invest in other activities (preening and self-feeding) away from the nest site. As numerous bird species increase alarm calling rates in response to nest predators (Hollén & Radford 2009), such trait-mediated indirect lethal effects may thus be a common, but previously undetected, source of nest failure, particularly in areas with high nest predator density, such as towns and cities.

Under some circumstances grey squirrel presence at nest sites resulted in a significant reduction in parental blackbird provisioning rates, an important indicator of the potential to generate sublethal effects. Notably, analyses of spatial patterns in population trends and nest failure rates of widespread woodland bird species have identified the blackbird as one of the species whose population size is most likely to have been depressed by recent increases in grey squirrel numbers (Newson *et al.* 2010a). Previous analyses of grey squirrel impacts on bird populations have, however, focussed on direct predation effects (Newson *et al.* 2010a,b), and we provide strong evidence that such analyses should be expanded to incorporate sublethal effects.

CONSERVATION AND MANAGEMENT IMPLICATIONS

It seems likely that the lethal indirect trait-mediated effects that we document are common in many avian predator–prey systems. This has important implications for assessing the role of specific predators. Simple proportioning of predator impacts based on the relative frequency at which each species predates nests could generate biased estimates of predator impacts, with those of third-party predators (corvids in this case study) being over-estimated, and those of predators initiating such predation events being underestimated (domestic cats in this case study). Such biases could lead to investment in unwarranted predator control programmes, and failure to recognize the role of other predator species and thus insufficient conservation management. We recommend that lethal trait-mediated indirect effects are taken into account during future assessments of predator impacts on prey assemblages.

The potential for domestic cats to exert important sublethal effects on wildlife populations has long been recognized, but empirical evidence has been lacking until now (Beckerman, Boots & Gaston 2007). The novel evidence that we provide for such sublethal and lethal indirect trait-mediated effects has important implications for managing the impact of domestic cat populations on wildlife. In many regions of the globe, wildlife protection laws and voluntary guidelines indicate that domestic cat impacts can be significantly reduced by restricting the time period during which domestic cats are allowed outside, and

increasing the detectability of domestic cats by placing bells or other devices on collars. While empirical evidence suggests that these management techniques can reduce direct predation impacts (Ruxton, Thomas & Wright 2002; Nelson, Evans & Bradbury 2005), their consequences for the magnitude of sublethal effects remain unexplored and far less certain. Avian perception of predation risk can remain high even when predators are absent due to previous exposure (Cresswell 2008, 2011), and we find no evidence that parental provisioning rates return to normal even when the domestic cat model had been removed for a considerable period of time. In addition, devices that increase the detectability of domestic cats could increase the spatial extent over which birds perceive an increase in predation risk, thus increasing the exposure of breeding birds to sublethal effects. The most effective management option simultaneously to mitigate direct predation, sublethal and lethal indirect trait-mediated effects of domestic cats on avian populations is thus to house cats permanently indoors. Cats housed indoors require more care and attention from their owners than those with access to the outside, but the vast majority can adapt successfully to living permanently indoors (Hall, Bradshaw & Robinson 2002; Jongman 2007). In the UK, approximately 3% of cat owners house cats indoors (Sims *et al.* 2008), yet in North America between 50% and 60% of domestic cats owners do so as this is considered to reduce cats' injury and mortality rates arising from road traffic, fights with other cats and other animals, and disease (Rochlitz 2005). This marked regional variation in the willingness of cat owners to house cats indoors strongly suggests that in many regions, including the UK, there is considerable potential to further mitigate the impacts of domestic cats on avian populations although there are likely to be strong cultural barriers in achieving this.

Acknowledgements

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Supporting Information

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

Fig. S1. Mean rates of parent blackbird alarm calling and aggressive behaviour in response to each model species.

Fig. S2. Mean food load size following exposure to each model species

Table S1. Response of parent blackbirds to the two morphs of each model species.