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Tawny Owl *Strix aluco* response to call-broadcasting and implications for survey design

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ABSTRACT

Capsule: The use of call-broadcasting significantly increases the number of Tawny Owls *Strix aluco* detected in winter point counts, but requires careful survey design to avoid introducing potential sources of bias into population estimates.

Aims: To examine Tawny Owl response to call-broadcasting to aid survey design in national monitoring efforts.

Methods: A nocturnal survey was undertaken at 36 survey points over three nights in winter in Thetford Forest, England. Each survey consisted of four consecutive five-minute segments: a passive count, followed by three counts with the use of call-broadcasting.

Results: Few (4%) Tawny Owls were recorded during passive surveys, whereas the greatest response was during the first and second call-broadcast segments (49% and 36%, respectively). New detections declined to 11% in the final segment. Response was fastest at dusk, although time of night did not significantly affect the number of individuals detected. Male owls accounted for 79% of detections.

Conclusion: Our results show that ten minutes of call-broadcast surveying will detect 85% of responsive Tawny Owls, thus vastly improving detection compared to passive listening alone. However, simultaneous counts of geographically separated detections should be used to provide a minimum count and reduce potential double-counting of mobile individuals.

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Call-broadcasting has been used to improve the probability of detecting birds in count surveys for a variety of species (e.g. McLeod & Andersen 1998, Zimmerling & Ankney 2000, Jakob *et al.* 2010). The technique involves broadcasting recorded calls of conspecifics or interspecifics to elicit a response (Johnson *et al.* 1981) and is particularly useful when surveying species that are secretive, exist in low-density populations or are otherwise difficult to detect. However, call-broadcasting can introduce problems not associated with traditional passive counts. For example, the response of birds may vary according to aspects of survey protocol or technique, and include additional behaviours, such as responsive movement (Legare *et al.* 1999, Spear *et al.* 1999). There is also potential for birds to become habituated to broadcasts over time (Rosenstock *et al.* 2002, Conway & Gibbs, 2005, Barnes & Belthoff 2008). Understanding such factors is crucial in dealing with potential biases in estimates of population size or occurrence (Kéry & Schmidt 2008, Nichols *et al.* 2009).

In Britain, the Tawny Owl *Strix aluco* has experienced a sustained downward trend (11%) in numbers since 1967 (Robinson *et al.* 2015) and an overall contraction of 6% in breeding range between 1970 and 2010 (Balmer *et al.* 2013). Accordingly, it was added to the Amber list of Birds of Conservation Concern in the latest review (Eaton *et al.* 2015). However, Tawny Owl population status remains relatively poorly known in Britain, in part because the species is not well represented by current survey methods in national bird monitoring schemes, such as the Common Birds Census and Breeding Bird Survey. A large-scale Tawny Owl census carried out by the British Trust for Ornithology in 2005 (Freeman *et al.* 2006) incorporated call-broadcast surveying, although there has been little quantitative assessment of its use with Tawny Owls and important aspects of survey protocol remain untested. Thus, through field-based experiments, we compare aspects of Tawny Owl response between traditional, passive point count methods and call-broadcast methods, and investigate whether response varies throughout the night.

Methods

Study species

Tawny Owls are predominantly woodland birds and are relatively sedentary (Cramp 1985). Once established,

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individuals occupy exclusive territories that are vigorously defended all year round (Southern 1970, Percival 2002). Despite a broad vocal repertoire, the sexes can be distinguished with a reasonable level of certainty by two calls, the males making a drawn-out 'hoot' call and females responding with a sharp disyllabic 'ke-wick' (Southern 1970, Cramp 1985, Appleby *et al.* 1999). However, immature male owls can also make a similar call to that of adult females (Andersen 1961, Galeotti 2001). In Britain, Tawny Owls are particularly vocal during October and December (Percival 1990) when first-year birds are establishing territories and adults are defending theirs in readiness for the spring breeding season (Cramp 1985).

Study area

The study was conducted in the north of Thetford Forest (52.4603°N 0.6480°E), Norfolk and Suffolk, the largest lowland coniferous plantation in Britain. The study area covered approximately 1000 ha comprised mostly of coniferous plantation of varying ages (predominantly Corsican Pine *Pinus nigra* and Scots Pine *Pinus sylvestris*), with some mixed deciduous woodland (Eycott *et al.* 2006). The mosaic of forest types and growth stages is intersected by minor roads and firebreak trackways.

Establishing survey points

Based on an estimated Tawny Owl territory size of 10–15 ha (Southern 1970, Appleby & Redpath 1997) and audible calling range in closed woodland of up to 600 m (Lengagne & Slater 2002), a distance of 1 km between survey points was considered sufficient to limit the potential for repeat detections of the same individual. A total of 36 survey points was established by digitally overlaying the study area with a grid of 1 km^2 aligned to the British National Grid. The approximate centre of each 1 km^2 represented a survey point and the grid reference for each was calculated using ArcGIS (Environmental Systems Research Institute). The habitat within 350 m of each survey point, comprising 38.5 ha, was predominantly continuous woodland (median 97%, range 52–100%, n = 36). Survey points were located in the field using a map and handheld global positioning system unit (Garmin eTrex 30). The observer ventured approximately 50 m into the forest if the survey point was near to a busy road to reduce the effect of the sound of traffic on the ability to hear calling birds.

For logistical reasons, experiments were conducted over three nights during the last week of December 2014. This is towards the end of the period of greatest vocal activity (Percival 1990), when the majority of birds will be defending established territories before the start of the nesting season. Each night was divided into three survey periods defined as 'dusk' (18:00–21:00), 'midnight' (22:30–01:30) and 'dawn' (03:00–06:00), during each of which, surveys were carried out at four different points. As such, each of the 36 points was surveyed once during the entire three night period. In an attempt to control for the effects of spatial variation in habitat, Tawny Owl distribution and other potentially confounding factors, successive survey points were non-adjacent. Surveys were conducted on dry, still nights to avoid effects of adverse weather on Tawny Owl vocal activity (Lengagne & Slater 2002).

Survey procedure

At each survey point, a five-minute acclimatization period was observed to limit any potential effect of disturbance on the vocal behaviour of owls present (Bibby *et al.* 2000), after which a 20-minute survey was conducted recording each new individual detected throughout. The survey comprised four consecutive five-minute segments: a passive segment followed by three segments featuring call-broadcasting (referred to as CB1, CB2 and CB3). This linear survey design enabled an experimentally robust comparison of passive and call-broadcast techniques, and increased the power of statistical analyses. The total 20-minute period was divided into one-minute time intervals, with the observer recording the interval (1–20) of each new Tawny Owl detection and the type of call ('hoot' or 'ke-wick'). 'Hoot' calls were recorded as male and, due to difficulty distinguishing between immature male and adult female owls, the sex of 'ke-wick' calls was recorded as unknown. The approximate location was also noted on a map to help differentiate between individuals during the survey, and in an attempt to monitor the behaviour of responsive individuals and identify possible repeat detections between points.

Call-broadcast survey segments comprised a recording featuring 'hoot' and 'ke-wick' calls for the first minute, and passive listening for the remaining four minutes. Using a CEM DT-805 Noise Meter, a handheld speaker system (Walsoon Outdoor, Model: CP-550) was set to a volume equivalent to 90 dB at 1 m distance, matching the sound pressure level for Tawny Owls estimated by Lengagne & Slater (2002). In a clockwise direction, the recording was broadcast at chest-height in the four cardinal compass points for 15 seconds each, starting with North.

Statistical analysis

Variation in the number of Tawny Owls detected during surveys was examined using a generalized linear mixed model (GLMM) using the R package lme4 (Bates *et al.* 2015) with log link function and Poisson error structure. The number of individuals detected was the response variable, fixed factors were night, survey period (dusk, midnight, dawn) and survey segment (passive, CB1, CB2, CB3) and survey point was fitted as a random factor. Non-significant factors were removed from the model by backwards deletion and the estimates are given at the point of removal. To investigate whether the time taken to respond to call-broadcasting varied throughout the night, we pooled data across nights and compared the number of individuals detected during the four minutes before and after the first minute of CB2 in separate Wilcoxon rank-sum analyses for each survey period. To determine if survey points at which Tawny Owls were absent were distributed unevenly between survey periods, we compared the proportion of occupied points using chi-square analysis. All analyses were performed using R version 3.3.2 (R Core Team 2015).

Results

Tawny Owls were detected at 30 of 36 survey points (83%) in Thetford Forest. The proportion of survey points in which Tawny Owls were detected did not vary significantly among survey periods ($\chi^2 = 1.185$, df = 2, $P = 0.553$) and the mean (±se) number of individuals recorded at a single point was 1.6 ± 0.13, although as many as five were recorded at several points. Of the 102 individuals detected over three nights, the majority (79%) were male. Three owls were also observed circling above the sound source during call-broadcasting.

Table 1. A GLMM investigating the factors affecting the number of Tawny Owls detected in surveys comprised of passive and call-broadcast methods.

Variable	Level	Estimate	se	*Z*	*P*
(Intercept)		−1.848	0.542	−3.411	<0.001
Night	Night 1	0	0	–	–
	Night 2	−0.239	0.253	−0.943	0.345
	Night 3	−0.410	0.264	−1.553	0.120
Survey period	Dusk	0	0	–	–
	Midnight	−0.051	0.245	−0.207	0.836
	Dawn	−0.515	0.275	−1.873	0.061
Survey segment	Passive	0	0	–	–
	CB1	2.584	0.518	4.989	<0.001
	CB2	2.169	0.527	4.114	<0.001
	CB3	0.916	0.591	1.551	0.121

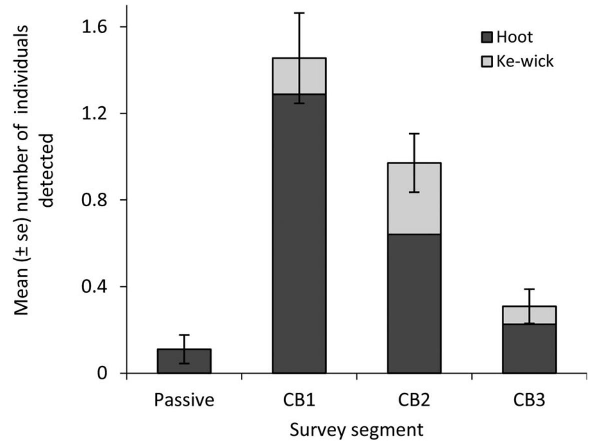

Figure 1. The mean (±se) number of Tawny Owls detected during each survey segment (CB, call-broadcast) showing relative numbers of males (hoot, $N = 81$) and females or immature males (ke-wick, $N = 21$).

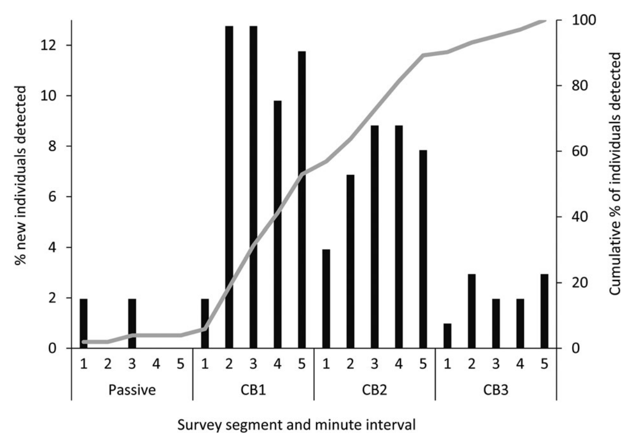

Figure 2. The percentage and cumulative percentage of initial Tawny Owl detections within successive minute intervals of the entire survey.

The number of Tawny Owls detected varied significantly between survey segments (Table 1; Figure 1). The first segment, a passive count, yielded only four individuals (all male), representing 4% of the number detected in the entire survey (Figure 2). The number of individuals detected increased significantly with the use of call-broadcasting (Table 1). Around half (49%) of detections occurred in less than five minutes of call-broadcasting and the number of new owls recorded declined steadily in subsequent segments (36% in CB2 and 11% in CB3; Figure 2). While survey period (i.e. time of night) did not significantly affect the number of individuals detected (Table 1), the speed with which owls responded to call-broadcasts was fastest at dusk, when significantly more individuals were detected in CB1 than in CB2 (Wilcoxon rank-sum analysis, $z = -1.980$, $P = 0.048$; Figure 3).

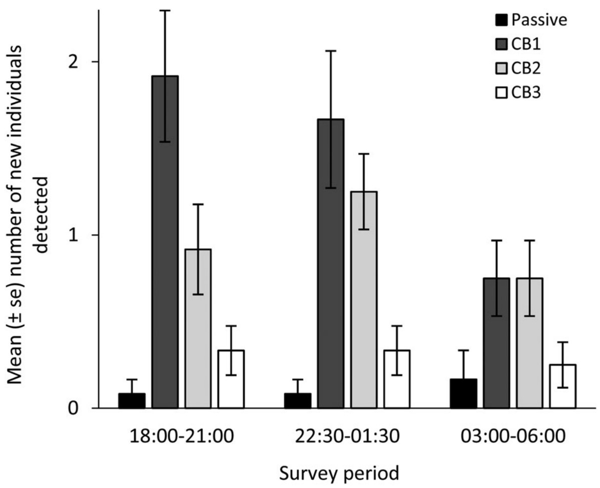

Figure 3. The mean (±se) number of new individual Tawny Owls detected during each survey segment (CB, call-broadcast) across three nocturnal periods.

Discussion

The number of Tawny Owls detected in passive surveys was low, reflecting the underlying difficulty of surveying species that are secretive or otherwise elusive. While many avian species have been shown to respond well to the recorded calls of conspecifics, our results indicate the technique is particularly effective with Tawny Owls, even compared to other nocturnal owls (Debus 1995, Conway & Simon 2003, Olson *et al.* 2005, Wintle *et al.* 2005). Although we did not know absolute numbers of individuals at survey points, our results support studies by Redpath (1994) and Freeman *et al.* (2006), both of which report Tawny Owl response rates of over 90% within 15 minutes of call-broadcast surveying. Individuals that responded to call-broadcasting did so quickly, particularly during the dusk survey period, when the speed of response was fastest. This did not significantly affect the number of detections during surveys, however, and diel variation in Tawny Owl responsiveness is apparently less than for other raptors (Kimmel & Yahner 1990, McLeod & Andersen 1998, Conway & Simon 2003).

In Freeman *et al.* (2006), the large majority of Tawny Owls were detected in the first few minutes of the survey, following a single episode of call-broadcasting. We also observed a strong response during the four-minute listening periods, but there was a shallow decline in new detections over the entire survey. This implies that some birds remained undetected until late in the survey. Response to playback is likely to be less vigorous and potentially delayed in low status individuals (Galeotti 1998). In addition, however, the circling behaviour of a number of owls above the sound source indicates that they were drawn towards the surveyor. Movement towards rivals (or perceived rivals) is typical of owls (Debus 1995) and, in the present study, a proportion of individuals may have originated from further away than their point of detection or, following initial detection, remained within audible range but moved to a different position in relation to the surveyor. Similarly, the response of less dominant individuals may have involved movements away from the surveyor. While we believe a distance of 1 km in closed woodland will have minimized the potential for repeat detections of the same individual between survey points, we cannot rule out instances of double-counting as a result of movement during surveys, particularly towards the ends of surveys if this behaviour increases as the number of calling birds accumulates.

Our results suggest there is considerable variation in detectability between male and female Tawny Owls. Almost 80% of responses were male 'hoot' calls. While male Tawny Owls have been shown to respond equally often to male and female calls, females are less responsive to the calls of males (Appleby *et al.* 1999). Consisting of both male and female calls, our call-broadcast recording may have been more effective in eliciting a response from males than females. However, this cannot account fully for the large disparity in numbers and we expect that our results represent natural variation in vocal activity. By December, pair formation has occurred and female Tawny Owls are significantly less responsive to the calls of conspecifics than at other times of the year (Redpath 1994). In contrast, both adult male Tawny Owls and those in their first breeding season may be particularly vocal in order to defend and establish territories (Appleby *et al.* 1999).

Implications for survey design

Our findings are limited by the short-time frame over which the study was conducted. Nevertheless, the results show that, compared to passive methods, call-broadcasting greatly improves the detection of Tawny Owls in winter surveys. This study also raises important issues concerning the use of call-broadcasting, with implications for survey design.

The number of detections was consistently lower during the minute-long playback period, likely indicating either reduced vocal activity of owls, or a reduced ability of the observer to detect calling birds. This clearly demonstrates the importance of intervening silent periods during call-broadcast surveys, and a series of short broadcast repetitions alternating with passive listening is an appropriate strategy for Tawny Owl surveys. Simultaneous counts of geographically separated detections should be used to provide a minimum count and reduce potential double-counting of mobile individuals. To survey when call-broadcasting is most effective, we recommend winter surveys are conducted between one hour after local sunset and two hours before midnight. Durations of 5 minutes (Zuberogoitia & Martínez Clement 2000), 10 minutes (Percival 1992) and 30 minutes (Redpath 1994, Freeman *et al.* 2006) have been suggested, however the effects of duration in call-broadcast surveys remain unclear. This aspect of survey design may represent a trade-off between detecting all responsive individuals and increasing the potential for double-counting, leading to inflated population estimates (Miller *et al.* 2012). While the argument for increasing survey duration is often justifiable in comparatively low-responsive species, we argue it could compromise data obtained using call-broadcasting in Tawny Owl surveys. Spacing between survey points presents a similar trade-off and should be based on survey objectives. For example, a spacing of 1 km between points may be reduced if the primary objective is to estimate Tawny Owl occupancy with high reliability, or increased if the primary objective is to estimate abundance. The use of a recorded call of a male from outside the study area has been shown to provoke a stronger aggressive response than to a neighbouring male (Galeotti & Pavan 1991), suggesting that call-broadcasting can maximize the response rate and therefore increase the detection of territorial birds.

Further research is needed to refine the use of call-broadcasting in Tawny Owl surveys. A key assumption is that individuals do not move prior to, or following, detection. It is important to examine the degree to which Tawny Owls are likely to violate this assumption and potentially to assess the degree of over-estimation of the number of birds present. Experiments in occupied territories, for example where known individuals can be tracked (e.g. Sunde & Bølstad 1999) or have been identified from spectrographic analysis of their calls (e.g. Galeotti & Pavan 1991), would allow the calculation of actual detection rates, help to understand patterns in responsive movements during surveys and determine detection distances. The findings of previous studies examining the influence of time of year on Tawny Owl response to call-broadcasting are inconsistent (e.g. Redpath 1994, Zuberogoitia & Martínez Climent 2000). Thus, repeat experiments are desirable, particularly throughout the breeding season. Habitat type and structure influence Tawny Owl population density and various aspects of behaviour (Hirons 1985, Hardy 1992, Redpath 1994), including response to call-broadcasting (Redpath 1994). This warrants further investigation in order that environmental factors can be accounted for in aspects of survey design, such as duration and spacing between survey points. In order to better understand data obtained using call-broadcasting, it would also be useful to further elucidate the potential interaction between aspects of demography such as sex, age class and breeding status (e.g. paired versus unpaired) in Tawny Owl vocal activity.

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References

Andersen T. 1961. En nordsjaellansk Natugle-bestand (*Strix alcuo*) i yngletiden [A population study of tawny owls in northern Zeeland, studied in breeding season]. *Dansk. Om. Foren. Tidsskr* **55:** 1–55. [In Danish]

Appleby, B.M. & Redpath, S.M. 1997. Variation in the male territorial hoot of the Tawny Owl *Strix aluco* in three English populations. *Ibis* **139:** 152–158.

Appleby, B.M., Yamaguchi, N., Johnson, P.J. & Macdonald, D.W. 1999. Sex-specific territorial responses in Tawny Owls *Strix aluco*. *Ibis* **141:** 91–99.

Balmer, D.E., Gillings, S., Caffrey, B.J., Swann, R.L., Downie, I.S. & Fuller, R.J. (eds) 2013. *Bird Atlas 2007–11: The Breeding and Wintering Birds of Britain and Ireland*. BTO Books, Thetford.

Barnes, K.P. & Belthoff, J.R. 2008. Probability of detection of Flammulated Owls using nocturnal broadcast surveys. *J. Field Ornithol.* **79:** 321–328.

Bates, D., Maechler, M., Bolker, B. & Walker, S. 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Soft.* **67**(1): 1–48.

Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S.H. 2000. *Bird Census Techniques*, 2nd edn. Academic Press, London.

Conway, C.J. & Gibbs, J.P. 2005. Effectiveness of call-broadcast surveys for monitoring marshbirds. *Auk* **122:** 26–35.

Conway, C.J. & Simon, J.C. 2003. Comparison of detection probability associated with Burrowing Owl survey methods. *J. Wildl. Manage* **67:** 501–511.

Cramp, S. (ed.) 1985. *The Birds of the Western Palearctic*, Vol. 4. Oxford University Press, Oxford.

Debus, S.J.S. 1995. Surveys of large forest owls in northern New South Wales: methodology, calling behavior and owl responses. *Corella* **19:** 38–50.

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.

Eycott, A.E., Watkinson, A.R. & Dolman, P.M. 2006. The soil seedbank of a lowland conifer forest: the impacts of clear-fell management and implications for heathland restoration. *Forest Ecol. Manag.* **237:** 280–289.

Freeman, S.N., Balmer, D.E. & Crick, H.Q.P. 2006. On the censusing of Tawny Owl *Strix aluco*. *Bird Census News* **19:** 58–62.

Galeotti, P. 1998. Correlates of hoot rate and structure in male tawny owls *Strix aluco*: implications for male rivalry and female mate choice. *J. Avian Biol.* **29:** 25–32.

Galeotti, P. 2001. *Strix aluco* Tawny Owl. Birds of Western Palearctic, Update 3: 43–77. Oxford University Press, Oxford.

Galeotti, P. & Pavan, G. 1991. Individual recognition of male tawny owls (*Strix aluco*) using spectrograms of their territorial calls. *Ethol. Ecol. Evol.* **3:** 113–126.

Hardy, A.R. 1992. Habitat use by farmland Tawny Owls *Strix aluco*. In Galbraith, C.A., Taylor, I.R. & Percival, S. (eds) *The Ecology and Conservation of European Owls*, 55–63. Joint Nature Conservation Committee, Peterborough.

Hirons, G.J.M. 1985. The effects of territorial behaviour on the stability and dispersion of Tawny Owl (*Stryx aluco*) populations. *J. Zool., Lond. (B)* **1:** 21–48.

Jakob, C., Ponce-Boutin, F., Besnard, A. & Eraud, C. 2010. On the efficiency of using song playback during call count surveys of Red-legged partridges (*Alectoris rufa*). *Eur. J. Wildl. Res.* **56:** 907–913.

Johnson, R.R., Brown, B.T., Haight, L.T. & Simpson, J.M. 1981. Playback recordings as a special avian census technique. In Ralph, C.J. & Scott, J.M. (eds) *Estimating Numbers of Terrestrial Birds Pages, Studies in Avian. Biology* **1:** 68–75.

Kéry, M. & Schmidt, B.R. 2008. Imperfect detection and its consequences for monitoring for conservation. *Community Ecol* **9:** 207–216.

Kimmel, J.T. & Yahner, R.H. 1990. Response of Northern Goshawks to taped conspecific and Great Horned Owl calls. *J. Raptor Res.* **24:** 107–112.

Legare, M.L., Eddleman, W.R., Buckley, P.A. & Kelly, C. 1999. The effectiveness of tape playback in estimating Black Rail density. *J. Wildl. Manage* **63:** 116–125.

Lengagne T. & Slater, P.J.B.S. 2002. The effects of rain on acoustic communication: Tawny Owls have good reason for calling less in wet weather. *P. Roy. Soc. Lond. B Bio.* **269:** 2121–2125.

McLeod, M.A. & Andersen, D.E. 1998. Red-shouldered Hawk broadcast surveys: factors affecting detection of responses and population trends. *J. Wildl. Manage.* **62:** 1385–1397.

Miller, D.A., Weir, L.A., McClintock, B.T., Grant, E.H.C., Bailey, L.L. & Simons, T.R. 2012. Experimental investigation of false positive errors in auditory species occurrence surveys. *Ecol. Appl.* **22:** 1665–1674.

Nichols, J.D., Thomas, L. & Conn, P.B. 2009. Inferences about landbird abundance from count data: recent advances and future directions. In Thompson, D.L., Cooch, E.G. & Conroy, M.J. (eds.), *Modeling Demographic Processes in Marked Populations*, 203–238. Springer, US.

Olson, G.S., Anthony, R.G., Forsman, E.D., Ackers, S.H., Loschl, P.J., Reid, J.A., Dugger, K.M., Glenn, E.M. & Ripple, W.J. 2005. Modeling of site occupancy dynamics for northern spotted owls, with emphasis on the effects of barred owls. *J. Wildl. Manage.* **69:** 918–932.

Percival, S.M. 1990. *Population trends in British Barn Owls,* Tyto alba*, and Tawny Owls,* Strix aluco*, in relation to environmental change*. Research Report 57. BTO, Tring.

Percival, S. 1992. *Methods of Studying the Long Term Dynamics of Owl Populations in Britain*. Ecology and conservation of European Owls. UK Nature Conservation No. 5. Joint Nature Conservation Committee, Peterborough.

Percival, S.M. 2002. Tawny owl *Strix aluco*. In Wernham, C.V., Toms, M.P., Marchant, J.H., Clark, J.A., Siriwardena, G.M. & Baillie, S.R. (eds) *The Migration Atlas: Movements of the Birds of Britain and Ireland*, 432–433. T. & A.D. Poyser, London.

R Core Team. 2015. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available from: https://www.R-project.org/.

Redpath, S.M. 1994. Censusing Tawny Owls *Strix aluco* by the use of imitation calls. *Bird Study* **41:** 192–198.

Robinson, R.A., Marchant, J.H., Leech, D.I., Massimino, D., Sullivan, M.J.P., Eglington, S.M., Barimore, C., Dadam, D., Downie, I.S., Hammond, M.J., Harris, S.J., Noble, D.G., Walker, R.H. & Baillie, S.R. 2015. *BirdTrends 2015: Trends in Numbers, Breeding Success and Survival for UK Breeding Birds* [online]. Research Report 678. BTO, Thetford. Available from: http://www.bto.org/birdtrends [Accessed 14 May 2016].

Rosenstock, S.S., Anderson, D.R., Giesen, K.M., Leukering, T. & Carter, M.F. 2002. Landbird counting techniques: current practices and an alternative. *Auk* **119:** 46–53.

Southern, H.N. 1970. The natural control of a population of tawny owls (*Strix aluco*). *J. Zool.* **162:** 197–285.

Spear, L.B., Terrill, S.B., Lenihan, C. & Delevoryas, P. 1999. Effects of temporal and environmental factors on the probability of detecting California black rails. *J. Field Ornithol.* **70:** 465–480.

Sunde, P. & Bølstad, M.S. 1999. A telemetry study of the social organization of a tawny owl (*Strix aluco*) population. *J. Zool.* **263:** 65–76.

Wintle, B.A., Kavanagh, R.P., McCarthy, M.A. & Burgman, M.A. 2005. The magnitude and management consequences of false negative observation error in surveys of arboreal marsupials and large forest owls. *J. Wildl. Manage.* **69:** 905–917.

Zimmerling, J.R. & Ankney, C.D. 2000. A technique that increases detectability of passerine species during point counts. *J. Field Ornithol.* **71:** 638–649.

Zuberogoitia, I.A. & Martínez Clement, J.A. 2000. Methods for surveying Tawny Owl *Strix aluco* populations in large areas. *Biota* **1:** 79-94.