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Variation in productivity and territory occupancy in an Eagle Owl *Bubo bubo* population

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Source-sink dynamics refer to systems with some units as sources of juveniles, and others as sinks. The same pattern can theoretically occur at a small spatial scale, within single populations. Under these circumstances, varying quality of breeding habitats/territories determines different levels of survival and/or reproduction, which in turn result in varying contributions of territories to the population dynamics. Territory occupancy has been proposed as an indirect measure of habitat quality. Here, we used territory occupancy and productivity from a long-term monitoring of an Eagle Owl *Bubo bubo* population in NW Italy to (i) show how different contributions to population dynamics may characterize territories over limited geographical scale in a strongly territorial species, and (ii) investigate the potential use of territory occupancy as a proxy for habitat quality in this species. Three out of 10 territories appeared to produce most fledglings (potential sources), whereas the others were characterized by extremely low productivity (possible sinks). The overall productivity is likely to nearly balance mortality, but the general equilibrium masks complex variation in the contributions of territories to the population dynamic. Territory occupancy was affected by average productivity, and thus long-term occupancy could be used as a proxy for habitat quality. In long-lived and scarce territorial species, such as the Eagle Owl, preservation of suitable conditions at key territories can be crucial for the population survival.

1. Introduction

Source-sink dynamics represent a common pattern in many animal and plant populations (Hanski 1998, Hanski & Gaggiotti 2004). In theory, bird species may persist as metapopulations, including patches of population sources (high-quality patches which allow the population to increase), sinks (low-quality patches unable to support a population without immigration) and pseudo-sinks (which appear sinks, because immigration maintains population levels above carrying capacity, but are sources). The above categories could often be identified with different population units, each one including a varying number of breeders. However, in strictly territorial species the quality of occupied territories, each hosting only one pair, may condition the breeding success, survival and/or other demographic parameters, thus determining the potential demographic contribution of a given site to a population and potentially creating a source-sink pattern at a considerably finer scale than usually supposed for most species (Lande 1987). Source-sink dynamics at the territory level have been reported for the Florida Scrub Jay *Aphelocoma coerulescens* and Siberian Jay *Perisoreus infaustus* (Breininger & Carter 2003, Nystrand *et al.* 2010) and are likely to occur in a number of other bird species, including raptors (Lande 1987, 1988, Liberatori & Penteriani 2001, Amar *et al.* 2012).

The functioning of individual territories as sinks or sources, and thus their contribution to general population dynamics, is determined by territory quality. This is because breeding output and survival are affected by habitat quality; pairs breeding in high-quality territories experience high breeding output (Newton 1998, Sergio *et al.* 2003, Förschler *et al.* 2005, Brambilla *et al.* 2010, Brambilla & Ficetola 2012). Territory quality is often associated with territory occupancy, a pattern confirmed for, e.g., the Black Kite *Milvus migrans* and Sparrowhawk *Accipiter nisus* (Newton 1991, Sergio & Newton 2003). Hence the temporal occupancy of a territory can be considered a proxy for territory quality.

Our model species, the Eagle Owl *Bubo bubo*, is the largest nocturnal raptor in the Palaearctic region. Previous studies have shown average productivity to vary among territories (Penteriani *et al.* 2004, Bionda & Brambilla 2012), with contributions to the general population dynamics varying accordingly in different years, and a higher occupancy rate of successful territories (Marchesi *et al.* 2002). Eagle Owls also show source-sink dynamics, as demonstrated by sink populations maintaining stable numbers thanks to massive immigration (Schaub *et al.* 2010). Although population models for the species have been proposed at a regional scale and heterogeneity in productivity at the site level is not new in the Eagle Owl (Penteriani *et al.* 2002), until now virtually no study has analyzed heterogeneity in habitat quality (and hence productivity) in terms of explicit modelling of population dynamics within a single population. We assume that different contributions to the general population dynamics, as within source-sink systems, will be found within a population (Nystrand *et al.* 2010) on the basis of large variation in the average productivity across different territories related to different habitat quality (Sergio & Newton 2003, Penteriani *et al.* 2004, Bionda & Brambilla 2012).

We used a demographic model to assess whether source-sink dynamics are likely to occur within a given population by calculating a territory-specific hypothetical growth rate (the growth rate of a virtual population entirely experiencing the same conditions within a given territory). We considered our study system a single population because distances among adjacent breeding territories was always less than 24 km, being lower than common dispersal distances covered by individuals of the focal species (Olsson 1997, Aebischer *et al.* 2010; but see Delgado *et al.* 2010). Our study is, to our knowledge, the first attempt to demonstrate how the preservation of conditions at key breeding sites contributes to the conservation of an Eagle Owl population. We also assessed whether occupancy can indicate habitat quality. If occupancy is correlated with average productivity, the former could be taken as a proxy for habitat quality.

2. Material and methods

2.1. Study area and field work

The study area (2,255 km^2, elevation 192–4,634 m. a.s.l., 64% of territory above 1,000 m; Fig. 1) is located in the central-western Italian Alps (Province of Verbano-Cusio-Ossola, Piedmont, 8°19'N, 46°06'E). Annual precipitation averages 1,594 mm (Biancotti & Bovo 1998). The study area includes woodlands (52% of the surface), alpine meadows (11%), shrublands (9%), rocky outcrops and cliffs (8%), grasslands and cultivations (7%), wetlands (4%) and urbanized areas (3%), and is one of the least urbanized areas in Italy (Bionda & Brambilla 2012). The study area is delimited by a lowland plain in the south (an area unsuitable for owls), Lake Maggiore in the east, and by high mountains on northern and western sides. The Eagle Owl population considered here is rather isolated on the southern side of the area, because of the ecological and geographical boundaries, whereas at the northern and especially northern-

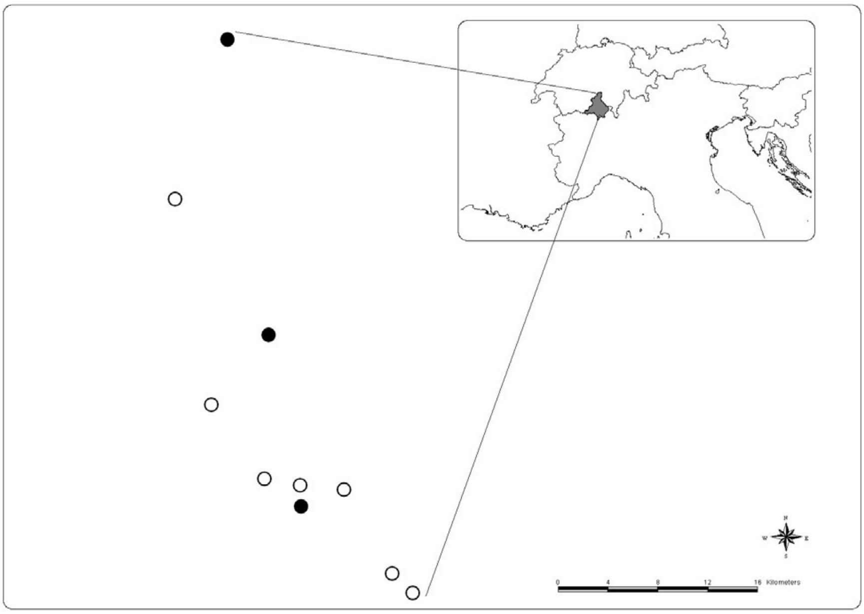

Fig. 1. Presumed source (black dots) and sink (open circles) territories of Eagle Owls within the study area in NW Italy.

eastern boundary there is more likely continuity with the neighbouring Swiss populations. The overall Eagle Owl population accounted for 10–12 breeding pairs during the study period; three breeding territories located towards the boundaries of the area were not surveyed during this study.

From 1996 to 2011, ten Eagle Owl breeding territories (each including 1–3 alternative nest sites) were checked during November–February to assess the occupancy (by means of methods commonly employed for the species, such as listening to calls, using playback, searching for day-roosting birds or for recent signs of presence) and in late May–July to estimate reproductive success. Data included 122 occupied breeding territories across all years, and productivity data for 103 breeding attempts (territory occupied and checked for offspring). For some years/territories data were not collected due to the lack of survey, and in other years some territories were not occupied. We calculated average productivity for each territory and for pooled overall data.

For further details on the study area and population, field methods, and environmental determinants of breeding performances, see Bionda and Brambilla (2012).

2.2. Statistical analyses

We provided an estimate of how many juveniles were contributed by the most productive 30% and 50% of the territories to assess the disproportional contribution of individual territories to overall breeding performances (Sergio & Newton 2003). We calculated the above estimates also considering the average productivity calculated only for the period of 1996–2007 (Bionda & Brambilla 2012), as the most recent years (2008–2011) were characterized by low productivity (0.39 fledged juveniles per breeding attempt) and by low data availability (4.5 breeding attempts per year known from this period). We then modelled the effect of productivity on territory occupancy by means of a logistic regression analysis, with average productivity as a factor, and occupancy (occupied or not) as a dependent variable (Venables & Ripley 2002).

We derived the mortality values from an earlier study on population modelling for Italian Eagle Owl populations (Gustin *et al.* 2009). This study used an estimated annual mortality of 55% in the first, 30% in the second and 12% from the third year onwards for both sexes; these values fall within the range reported in literature and were believed to be applicable also for the Italian Eagle Owl populations, although they were derived from data collected in other countries. When specific in-

Table 1. Average productivity and occupancy of the breeding territories and relative sample size (in parentheses; for productivity number of breeding attempts, for occupancy number of survey years).

Territory	Average productivity ± SE	Occupancy
1	1.00 ± 0.18 (16)	1 (16)
2	0.00 ± 0.00 (4)	0.67 (6)
3	1.63 ± 0.33 (16)	1 (16)
4	0.75 ± 0.41 (8)	0.64 (14)
5	0.00 ± 0.00 (7)	1 (7)
6	0.57 ± 0.30 (10)	0.46 (13)
7	1.17 ± 0.30 (12)	1 (12)
8	0.70 ± 0.33 (10)	0.91 (11)
9	0.36 ± 0.20 (14)	0.93 (15)
10	0.00 ± 0.00 (6)	0.5 (12)
Overall	0.76 ± 0.10 (103)	0.82 (122)

formation is missing, the use of values calculated elsewhere (but thought to be comparable to the true values for the study species/site) is necessary, and is often done in population modelling studies (Katzner *et al.* 2006, Amar *et al.* 2011). Mortality values used in this study and obtained from Gustin *et al.* (2009) were slightly higher than those reported from Sweden (Olsson 1997) and lower than those reported from a Swiss population suffering extremely high mortality due to a heavily humanized environment (Schaub *et al.* 2010). The impact of human activity in our study area is likely to be higher than in Sweden but lower than in the Swiss study; electrocution and collisions affect also our study population, but probably less than in the latter study (Schaub *et al.* 2010).

Given the lack of local data, we used the same mortality values for all territories. For each territory, we calculated the average breeding productivity and its standard error (hereafter SE; Table 1); productivity values were entered in the analyses. All parameters were set as constant as we were interested in obtaining an estimation of the growth rate with the only aim to assess the likely "average" function of individual territories within overall population dynamics: source (estimated growth rate r – SE > 0), sink (r + SE < 0), or "neutral" territory (r + SE > 0 and r – SE < 0; no territories fell within this category). We ran the analyses simulating an unlimited and large population to avoid effects of short-term extinction or reaching a carrying capacity on the estimated growth rate. We then modelled overall population dynamics using average overall productivity, and also annual average productivity calculated for 1996–2007 (see above). All analyses were re-run after both increasing and decreasing all mortality rates (first year, second year, from third year onwards) by 5%. We ran the models in Vortex 9.99b, with simulations over 100 years and high population values (100 individuals) to avoid biased growth rate due to short-term extinction and without limits due to carrying capacity.

3. Results

Average overall productivity was 0.76 ± 0.10 SE. Considering average values of productivity over the whole study period (1996–2011), the most productive 50% of territories produced 85% of all young, and the most productive 30% of the territories 61% of all young. Considering the average productivity values calculated over the period of 1996–2007, the most productive 50% of the territories produced 86% of all young, and for the most productive 30%, the number was 64% of all young.

Average productivity strongly affected the occupancy (logistic regression, intercept 0.51 ± 0.36; $\beta = 1.72 \pm 0.57$, $\chi^2 = 11.04$, $p = 0.001$; residual deviance 104.11 with 120 df). Seven out of ten territories experienced an extremely low productivity: according to the simulated territory-specific dynamics, they may have acted as sinks, whereas three territories had a higher average productivity and may have served as sources for the whole population (Table 1, Figs. 1–2).

The output of the overall population model suggested that the average productivity was likely to balance (or to nearly balance) the supposed mortality. For productivity during 1996–2011, the estimated growth rate was slightly negative ($r = -1.35 {*} 10^{-2} \pm 0.09 {*} 10^{-2}$; Fig. 2), whereas it was slightly positive using the average productivity for 1996–2007 ($r = 3.8 {*} 10^{-2} \pm 0.07 {*} 10^{-2}$).

Varying mortality levels showed somewhat different results (Fig. 2). An increase of all mortality values by 5% resulted in two of the three "source" territories to become putative sinks, whereas the estimated overall population growth

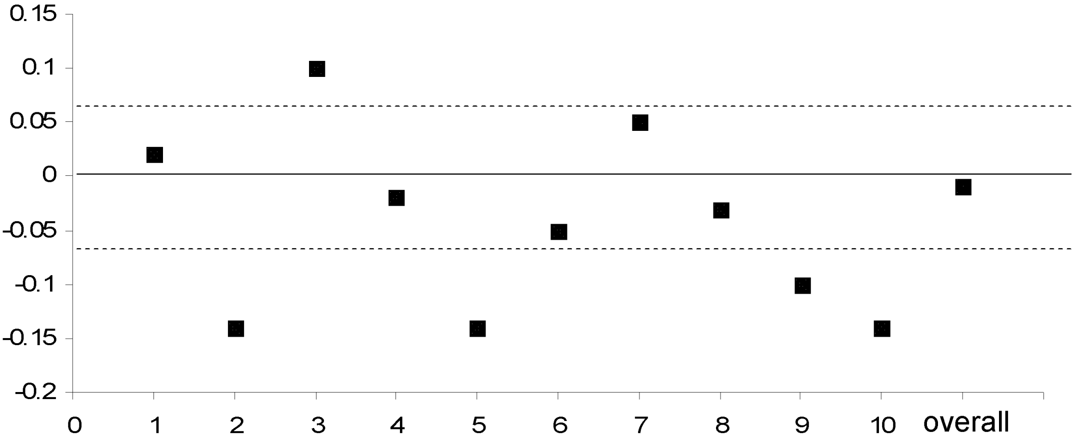

Fig. 2. Hypothetical growth rate for single territories and the overall population. X axis shows territory codes (as in Table 1), and Y axis shows the growth rate as calculated in Vortex (see text for details). Solid line represents population stability in the standard scenario, whereas dashed lines represent population stability in alternative scenarios (mortality values ± 5%). Territories with growth rate above population stability are putative sources, whereas those below are putative sinks.

rate became definitely negative ($r = -9.21*10^{-2} \pm 0.25*10^{-2}$). On the contrary, a decrease of all mortality values by 5% resulted in three "sink" territories to become putative sources, whereas the estimated overall population growth rate became definitely positive ($r = 5.19*10^{-2} \pm 0.02*10^{-2}$).

4. Discussion

We found that even at a small spatial scale, some territories in our Eagle Owl population served as source territories while others acted as sinks. The population dynamics over a limited geographical scale can be affected by the quality of individual territories within the same population, and the occupancy can be used as a proxy for territory quality. Due to the rather extreme average values of productivity and differences between territories we are confident in our interpretation of this general pattern. This was despite that we were forced to use (a) mortality values estimated from another population, and (b) the same values across all territories. Indeed, simulations carried out with ± 5% variation in mortality rates showed that (i) both "source" and "sink" territories would occur also within different scenarios; (ii) the "average" mortality values used apparently resulted in a good coherence with the observed population trend. The pattern would significantly change only with unsustainable mortality rates, such as the ones reported in Valais, Switzerland, which require a productivity of more than 17 fledglings per pair/year to maintain a stable population (Schaub *et al.* 2010). At the overall population level, differences in mortality could lead to re-estimates of the general dynamics: if mortality is higher than predicted, a higher immigration rate would be required to maintain the study population. However, this possibility does not affect the main conclusions of our study.

The disproportionate average productivity means that the most productive 50% of territories were likely to produce most of the young. Although similar patterns have been reported also for the Black Kite (*Milvus migrans*; Sergio & Newton 2003), Sparrowhawk (*Accipiter nisus*; Newton 1991) and Hobby (*Falco subbuteo*; Sergio & Bogliani 1999), the disproportionate contribution to the overall productivity observed in our study population seems even higher, further stressing the significant role of the quality of individual territories for the general population dynamics. Similarly, our results are even more extreme than the heterogeneous pattern reported for the species in France, where all pairs contributed to the annual production of juveniles during good years, but only a few pairs did so in poor years (Penteriani *et al.* 2004). In our study system, some territories apparently never fledged any young.

The output of the overall population model suggests that productivity is likely to balance mortality. This suggests population stability, which is confirmed by the almost stable number of breeding pairs in the study area. This general pattern masks more complex dynamics due to spatial variation in habitat quality and hence in breeding performances. Three territories had a high average productivity, whereas three others did not fledge any young in the 17 cases of known territory occupancy.

These peculiar patterns of variation in productivity have important conservation implications. A removal of the pair with the highest average productivity and hypothetical growth rate (territory 3; Table 1, Fig. 2) resulted in a change in the overall population dynamics from stability to decline. With the newly-calculated productivity (0.60 ± 0.09), with all other parameters constant, the growth rate in average overall productivity was definitely below zero ($r = –4.87*10^{–2} ± 1.40*10^{–2}$). The maintenance of suitable conditions at territories with very high reproductive rates is crucial for the conservation of the entire population: high quality territories contribute a disproportionately large number of offspring to the overall population. This makes the Eagle Owl particularly subjected to spatially-limited episodes of disturbance, or to local changes in habitat quality (Bionda & Brambilla 2012), which could result in population declines and eventual extinctions in the absence of compensation by immigration in the middle term (Schaub *et al.* 2010). The amount of rainfall during chick rearing, the so-called wetland interspersion index, and the cover of urban areas are important determinants of habitat quality via an effect on both fledging rate and breeding success (Bionda & Brambilla 2012).

Spatial variation in the productivity of Eagle Owls has been reported also from France and the Italian Alps, where landscape features affected the breeding performance between territories (Marchesi *et al.* 2002, Penteriani *et al.* 2004). Therefore, spatial variation in owl productivity, with consequent different contribution of individual territories to overall dynamics, may be common in Eagle Owl populations (Penteriani *et al.* 2002, 2004).

We suggest that territory occupancy may be used as a proxy to estimate territory quality and thus to evaluate the contributions of territories to overall population dynamics: territories known to be occupied for a long time without evidence of vacancy are likely to be particularly suitable for the species. These territories represent conservation priorities. Caution must be used when evaluating occupancy over a short time: one territory was occupied for seven years but did not produce any young (Table 1). Occupancy has been suggested as a measure of habitat quality on the basis of a correlation between breeding performance and occupation rate also in several other bird species (Sergio & Newton 2003), and long-term occupancy may be used as an indirect measure of quality if detailed data on habitat quality are missing.

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Huuhkajareviirien poikastuoton ja asuttamisen vaihtelu

Lähde-nieludynamiikka kuvaa systeemejä, joissa osa yksiköistä tuottaa nuorten yksilöiden ylijäämän, kun osa taas toimii nieluna tai ”valenieluna”. Samanlaista vaihtelua voidaan teoriassa tavata myös pienemmässä mittakaavassa, yksittäisen populaation sisällä, tilanteessa jossa reviirin laatu määrittelee yksilöiden selviytymistä ja jälkeläistuottoa, näiden edelleen vaikuttaessa populaatiodynamiikkaan eri tavoin. Reviirin asuttamisen on esitetty kertovan ympäristön laadusta.

Tutkimme huuhkajan (*Bubo bubo*) pitkäaikaista reviirin asuttamista ja tuottavuutta Pohjois-Italiassa (i) kuvaillaksemme, miten reviirien laatu määrittelee rajoittuneella maantieteellisellä alueella olevan populaation dynamiikkaa, ja (ii) selvittääksemme reviirin asuttamisen toimivuutta ympäristön laadun heijastajana.

Kolme kymmenestä reviiristä tuotti suurimman osan lentopoikasista ja olivat siten potentiaalisia lähdereviirejä. Loppuja luonnehti äärimmäisen alhainen poikastuotto, eli ne saattavat olla nieluja. Populaatiotasolla tuottavuus näytti tasapainottavan kuolleisuutta, mutta tasapainotila pitää sisällään monimutkaista reviirikohtaista vaihtelua tuottavuudessa. Reviirin asutus riippui keskimääräisestä jälkeläistuotosta, joten pitkäaikainen asuttaminen voi heijastaa ympäristön laatua. Pitkäikäisillä ja vähälukuisilla, territoriaalisilla lajeilla, kuten huuhkajalla, avainreviirien hyvien olosuhteiden säilyttäminen saattaa olla koko populaation säilymisen kannalta keskeistä.

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