Density fluctuations in an urban population of Tawny Owl *Strix aluco*: a long-term study in Rome, Italy

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Abstract

The population of Tawny Owls *Strix aluco* breeding in urban Rome, Italy, was studied from 1992 to 2001. Yearly density (range: 0.9–1.1 territories km^{-2}) was rather stable compared with data from central Europe, likely due to mild weather conditions and abundant food supply. The rate of territory occupation, regarded as estimator of density fluctuations, was non-linearly correlated with density and proportion of wooded and farmland areas, and not correlated with the proportion of built-up areas. In plots with owl density ranging from 2–4 territories km^{-2} all the breeding territories were stable over ten years. At decreasing density the lower rate of territory occupation was attributable to the large proportion of unsuitable habitat. Competition with neighbours and the consequent reduction of mean territory size may account for the lower territory stability at high densities, where the proportion of wooded areas is high. The proportion of farmland areas, which is a poor habitat for breeding but represent a suitable hunting ground, explains additional variance of the density fluctuations.

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Introduction

Raptors show some of the most stable densities known among birds, as can be documented from long-term studies. Breeding numbers generally do not fluctuate by more than 20 per cent of the mean over the period concerned (Wendland 1984, Newton 1991, Korpimäki & Norrdahl 1991). Population stability would be expected only in stable environments, not in habitats changing rapidly through vegetation succession or human action (e.g. Newton 1991).

Predators and prey are linked by mutual relationships that influence population dynamics of both guilds (Hanski & Korpimaki 1995). It is well known that fluctuations in prey abundance enhance responses of predators (e.g. Korpimäki & Norrdahl 1991). On the other hand, predators may play a critical role in dynamics of different prey species (e.g. Hanski & Korpimäki 1995). Based on their role in a predator/prey pattern, raptors may be splitted into two categories: resident, territorial generalists and nomadic specialists (Korpimäki & Norrdahl 1991). These two raptor categories show different responses to prey fluctuations, namely that functional responses are expected to be stronger in nomadic specialists (Korpimäki & Norrdahl 1991, Hanski & Korpimäki 1995). Resident generalists show a great ability to maintain stable populations and reproductive rate through the ability to exploit alternative prey thus regulating the interspecific competition for food.

In territorial, generalist raptors, the idea that breeding density is stable and feedback regulated, rather than fluctuating at random, is supported by the following findings: (i) the occurrence of surplus adults, able to breed, that occupy a territory only when it is available through death or removal of a previous occupant (Village 1983, Newton 1991); (ii) the rapid re-establishment of populations, after their removal by man, to the same level as previously (see Newton 1991); and (iii) the regular spacing of breeding pairs in areas with high nest supply (Southern 1970, Hirons 1985, Newton 1991).

Nest and food supply, competition, and weather condition seem to play a key role in the limitation of breeding numbers (Southern 1970, Village 1983,

Korpimäki & Norrdahl 1991, Newton 1991, Salvati 2002). Therefore, when some of these conditions are negligible in affecting population stability, it seems possible to attribute to the remaining conditions a great part of the effect on the variable itself. In the Mediterranean region it is accepted that (i) some rodent-eating raptors switch their diet toward alternative prey thus reducing the effect of fluctuating food (i.e. rodents), (ii) alternative prey (e.g. insects, reptiles, birds) are largely available and quite stable among years compared to central Europe (Gil-Delgado et al. 1995, Salvati 2002), and (iii) weather is stable and mild (Ranazzi et al. 2000b, Salvati 2002). These conditions are further enhanced in urban areas where the cyclic fluctuations of rodent prey are scarce and alternative prey are abundant (e.g. Galeotti 1994), climate is milder than in neighbouring countryside, and competitors and predators are scarce due to fragmentation and loss of suitable habitats (e.g. Ranazzi et al. 2000b, Salvati 2002).

The Tawny Owl *Strix aluco* is a territorial raptor that inhabits wooded, farmland, and urban habitats. Changes in population size of this resident, generalist raptor is mainly attributable to food supply, nest availability, and habitat characteristics (Southern 1970, Delmée et al. 1978, Wendland 1984). Tawny Owl may thus represent a model to study density fluctuations, especially in urban areas (Hirons 1985, Galeotti 1994, Redpath 1995, Ranazzi et al. 2000a).

In this paper we assess over ten years the rate of territory occupation as a measure of population dynamics in an urban population of Tawny Owls breeding in natural cavities in Rome, Italy. We test if the Rome population is more stable among years than more northern populations in central Europe. We further check relationships between the rate of territory occupation and density or habitat characteristics.

Methods

The fieldwork was carried out in the city centre (≈ 70 km^2) of Rome (41°53' N, 12°28' E) from 1992 to 2001. To assess territory occupation and breeding density we chose ten census plots including five strictly built-up areas and five urban parks (see Ranazzi et al. 2000a). All parks are mutually isolated by built-up areas. Vegetation of parks includes pines (*Pinus pinea*), cypresses (*Cupressus sempervirens*), cedars (*Cedrus* sp.), and isolated oaks (*Quercus* spp.) (Ranazzi et al. 2000a). Nests were usually located in natural cavities of old oaks and pines.

Territory size averaged 29.8±10.6 ha (n = 20) (Ranazzi et al. 2000a).

A preliminary census of all woodland patches (up to 0.2 hectares) and other potential breeding sites (e.g. ruderal areas, vegetable gardens, street trees) was made using aerial photographs. The field census was conducted by the male territorial 'hoot' playback stimulation performed in each potential site from November to August of each year (Redpath 1994), but different playback sessions were performed to obtain data on territory borders. Tawny Owls were contacted each year from the same playback spots. All individuals calling were located using 1:1000 and 1:10,000 maps. The "centre" of each territory (*sensu* Petty 1989) was determined as the nest site or, in a few cases, as the diurnal resting site. Diurnal visits in many territories searching for pellets, feathers, droppings, and other traces were performed monthly each year. During the post-fledging period (June–July in Rome) fledglings uttering the typical "begging call" often allowed us to locate the nest site (e.g. Wendland 1984, Redpath 1995). Non-breeding territories (e.g. no fledglings heard during breeding period and no other traces detected) with owls actively calling were however considered. Playbacks were not performed in autumn because the occurrence of fledglings able to hoot in the parent's territory may cause an overestimation of defended territories. All the neighbouring territorial pairs or single males were stimulated when an unknown Tawny Owl territory was located. According with Redpath (1995), the rapidity of male response to playbacks and the high number of visits regularly performed in each census plot may substantially reduce the likelihood that any territorial owls were missed.

For each census plot we collected each year the number of independent territories. All the territories defended by an adult male (irrespective of the presence of a female) were considered as independent (Ranazzi et al. 2000a). The rate of territory occupation over the entire study period, used as estimator of changes in population size, was obtained as the sum of total number of defended territories through the study period divided by the maximum number of independent territories multiplied by number of study years. In stable populations all territories are actively defended over long-time and maintain their original borders. Density was calculated for each census plot by the nearest neighbour distance (n.n.d.) method (Ranazzi et al. 2000a). Spacing among territories was computed using the "centre" of each territory (Petty 1989). We used this method to achieve comparable estimates of density and habitat
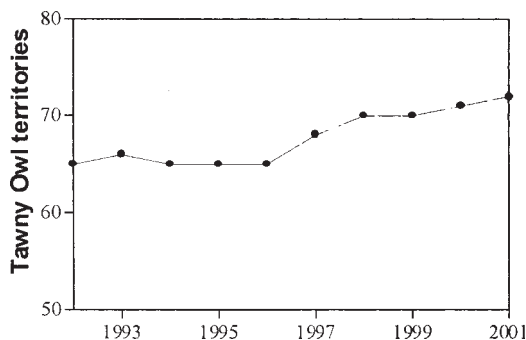
Figure 1. Density fluctuations of urban Tawny Owls over ten years (1992–2001) in Rome, Italy.
Täthetsfluktuationer hos urbana kattugglor under tio år (1992–2001) i Rom, Italien.
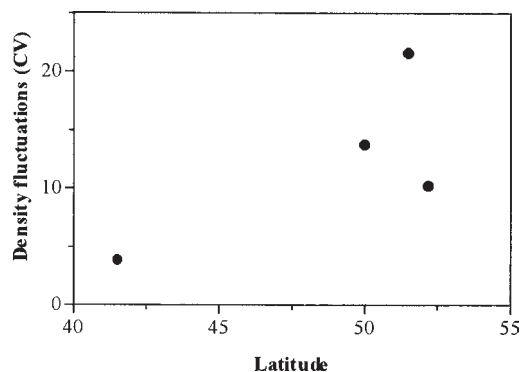

Figure 2. Coefficient of variation of territory density measured over long-term periods in four populations of Tawny Owls breeding at different latitude in Europe (sources: Southern 1970, Delmée et al. 1978, Wendland 1984, this paper).
Variationskoefficienten för revirtäthet under långa perioder i fyra populationer av häckande kattugglor på olika breddgrader i Europa (källor: Southern 1970, Delmée et al 1978, Wendland 1984, denna uppsats).

proportions in each census plot. Surfaces of built-up areas, farmlands, and wooded areas were measured across the whole 'n.n.d. area' using aerial photographs and VIDEOPLAN KONTRON PC package. Correlations between population or habitat variables and density fluctuations were performed using non-linear regressions. Curve fits were obtained using PRISM 2.0 (GraphPad Software, 1995) PC package.

Results

Based on a minimum of 65 territories continuously censused in inner Rome (1992–2001), population density ranged (Figure 1) from 0.9 to 1.1 territories km^{-2} (CV = 3.8%). The coefficient of variation calculated on the mean value of yearly density was lower than those recorded in other long-term studies performed in central Europe (Figure 2).

Density fluctuations in different sub-areas (Table 1) reflects differences at the habitat-level. In strictly urban areas, a comparable increase of occupied territories was observed in three strictly built-up plots, while in urban parks owl territories were remarkably stable.

Table 1. Density fluctuations, expressed as rate of territory occupation, of Tawny Owls in different census plots in urban Rome, Italy.
Täthetsfluktuationer uttryckt som andelen ockuperade revir av kattuggla i olika inventeringsytor i urbana Rom.

Census plot *Inventeringsområde*	Density *Täthet* (territories km^{-2})[a]	Territory occupation *Ockuperade revir* (%)	Max no. independent territories censused *Högsta antal oberoende revir*
City-centre *centrum*	1.2	83.3	6
Flaminio district	2.1	95.0	10
Nomentano district	2.0	91.4	8
Monteverde district	2.2	100.0	7
Villa Pamphili	2.9	100.0	9
Archaeological park	3.2	100.0	10
Verano cemetery *gravplats*	3.1	100.0	4
Monte Mario wood *skog*	3.8	100.0	12
Villa Borghese	4.9	85.0	8
Villa Ada	5.9	87.5	12

[a] Referring to spring 1999. *Avser våren 1999.*

Density fluctuations showed a non-linear dependence on population density (Figure 3) and on the proportion of wooded areas ($Y = 80.6 + 0.9x - 0.01x^2$, $r^2 = 0.57$, $p < 0.05$, df = 7). The population was stable in plots with density ranging from 2.5 and 4.0 territories km^{-2}. The density fluctuations positively correlated with the proportion of farmlands ($Y = 79.6 + 0.6x - 0.004x^2$, $r^2 = 0.61$, $p < 0.05$, df = 7) and were not affected by the proportion of built-up areas ($Y = 93.1 + 0.31x - 0.005x^2$, $r^2 = 0.37$, $p > 0.05$, df = 7).

Discussion

Although the obvious limits imposed by the descriptive nature of this study (e.g. difficulties to manipulate breeding density in populations of Tawny Owls nesting in natural cavities) prevented us to determine the intrinsic rate of territory turnover at the individual level, this work provides data on population stability and on the effect of habitat variables at different environmental conditions on density fluctuations.

We provided indirect evidences that the stability of Tawny Owl populations increases from north to south, likely as a consequence of milder climate conditions and reduction of small mammal fluctuations (Ranazzi 2000b, Salvati 2002). Interestingly, these factors also stabilise owl breeding success in the Mediterranean basin (Ranazzi et al. 2000b).

Density fluctuations increase at both low and high densities. At decreasing density the low territory stability is a consequence of the availability of unoccupied, sub-optimal areas not defended by owls. Competition among neighbours reduces territory size and accounts for the low territory stability in plots at high density, confirming that territory size play a key role in regulating occupancy rate (Hirons 1985, Galeotti 1994, Redpath 1995).

Tawny Owl density strictly depends on the proportion of suitable habitats (Southern 1970, Hirons 1985, Petty 1989, Redpath 1995, Ranazzi et al. 2000a). High proportions of wooded areas increase competition among neighbouring owls and cause fluctuations in density. The proportion of farmland areas explains additional variance of density fluctuations. Farmland areas usually represent sub-optimal nesting habitats but are good hunting territories. These areas may be temporarily occupied by owl pairs at their first breeding attempt or by single males, and this leads to higher density fluctuations than those observed in closed woodlands (Redpath 1995).

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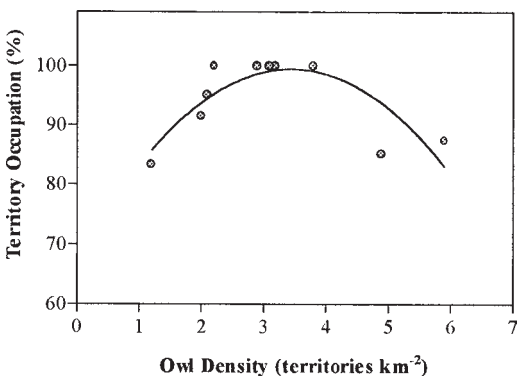
Figure 3. Relationship between the rate of territory occupation and owl density in ten census plots in urban Rome, Italy ($Y = 67.2 + 18.7x - 2.7x^2$, $r^2 = 0.68$, $p < 0.05$, df = 7).
Förhållandet mellan andelen ockuperade revir och uggletätheten i tio inventeringsytor i urbana Rom.

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Sammanfattning

Täthetsfluktuationer i en urban population av kattuggla Strix aluco*: en långtidsstudie i Rom, Italien*

Rovfåglar uppvisar några av de mest stabila bestånd som är kända bland fåglar, vilket dokumenterats i långtidsstudier. Antalet häckade par varierar vanligen inte med mer än 20 procent kring medelvärdet. Stabilitet förväntas dock bara i stabila biotoper, inte i biotoper som förändras genom successioner eller mänskliga ingrepp.

Predatorer och deras byten påverkar varandra. Mängden byten påverkar antalet predatorer, men predatorerna påverkar också dynamiken i bestånden av bytesdjuren. Predatorerna är av två slag: bofasta, revirhävdande generalister och nomadiska specialister. De bofasta generalisterna har stabila bestånd genom att de kan växla mellan alternativa byten, medan de nomadiska specialisterna fluktuerar kraftigt. De revirhållande generalisternas grundläggande stabilitet visas genom att det finns ett överskott av häckningsdugliga par som börjar häcka först när ett revir blir ledigt, att det sker en snabb återbesättning av reviren till tidigare nivå om fåglarna elimineras av människor samt att reviren är jämt spridda där tätheten är hög. Födotillgång, konkurrens och väderförhållanden begränsar antalet häckande par. I Medelhavsområdet kan predatorer som lever på smågnagare växla till insekter, reptiler och fåglar, som finns i riklig mängd, och dessutom är gnagarnas antalsväxlingar mindre och klimatet mildare än längre norrut.

Kattugglan är en revirhållande art som lever i skog, jordbruksmark och stadsmiljö. Täthetserna bestäms främst av tillgången på föda och boplatser samt biotopens övriga egenskaper. I denna uppsats studerar vi en population av kattugglor som häckar i naturliga håligheter i Rom, Italien. Vi undersöker populationens stabilitet under perioden 1992 – 2001 och jämför med populationer längre norrut i centrala Europa.

Undersökningsområdet ligger i centrala Rom (ca 70 kvadratkilometer) och består av fem bebyggda områden och fem parker, som är isolerade från varandra genom bebyggelse. Vegetationen i parkerna består av tallar, cypresser, cedrar och enstaka ekar. Ugglorna lokaliserades och deras revir bestämdes genom att spela upp hoandet under månaderna november till augusti. Vi gjorde också talrika besök året runt för att leta efter spybollar, fjädrar, spillning och andra spår. I juni och juli (flyggperioden i Rom) lyssnade vi efter ungarna tiggläten. Närhelst vi lokaliserade en tidigare okänd uggla gick vi runt och spelade upp hoanden för grannugglorna så att vi blev säkra på att det verkligen var en ny uggla. Det intensiva arbetet under alla årets månader alla tio åren gjorde att vi kraftigt kunde reducera risken att några ugglor missades.

För varje område gjorde vi en biotopbeskrivning som omfattade arealen bebyggd yta, jordbruksmark och trädbevuxen mark. Arealerna beräknades från flygfoton med programmet VIDEOPLAN KONTRON PC. Andelen ockuperade revir för hela perioden beräknade vi som summan av alla ockuperade revir dividerat med det maximala antalet revir som varit ockuperade något år multiplicerat med antalet inventeringsår. Sambanden mellan täthet och biotop gjordes med icke-linjära regressioner och kurvanpassning skedde med PRISM 2.0 PC.

Vi hade 65 revir som kontinuerligt följdes i undersökningsområdet alla tio åren. Tätheten varierade mellan 0,9 och 1,1 revir per kvadratkilometer (CV = 3,8%) (Figur 1). Denna variationskoefficient var lägre än vad man funnit i andra långtidsstudier i centrala Europa (Figur 2). Täthetsfluktuationerna i delområdena speglar biotopskillnader (Tabell 1). Täthetsvariationerna visade ett icke linjärt beroende av tätheten (Figur 3). Alla revir var alltid besatta vid tätheter från 2,5 till 4 revir per kvadratkilometer, medan den genomsnittliga beläggningen var lägre vid både lägre och högre tätheter. Det var ett icke linjärt samband med andelen skogsmark och ett positivt linjär samband med andelen jordbruksmark men inte något samband med andelen bebyggd areal.

Genom att undersökningen är rent deskriptiv och fåglarna inte individuellt märkta kan vi inte fastställa något om individomsättningen i de enskilda reviren. Vi kunde dock mäta populationens stabilitet och olika biotopers inverkan. Vi kunde också visa att kattugglepopulationers stabilitet ökar från norr mot söder. Detta är sannolikt en följd av gynnsammare klimat och mindre fluktuationer i gnagarbestånden. Intressant var att finna att fluktuationerna (andelen obesatta revir) ökade både vid låg och hög täthet. Detta tror vi beror på att det i områden med låg täthet finns ogynnsamma revir som besätts bara vissa år. Att det också fanns obesatta revir vid hög täthet tror vi beror på hård konkurrens mellan närliggande par som då och då utesluter att vissa revir ockuperas alla år.