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Long-term study on interactions between Tawny Owls *Strix aluco*, Jackdaws *Corvus monedula* and Northern Goshawks *Accipiter gentilis*

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We monitored the dynamics of owls, raptors and corvids within the 3400 ha of the Amsterdam Water Supply Dunes in the western Netherlands from 1961 through 2007. In the 1930s and 1950s, afforestation projects were initiated. In 1961 the first Tawny Owl nest was found, from whence the population increased steadily to stabilize in the 1970s at c. 24 pairs. Tawny Owl dynamics were affected by competition for nest sites with Jackdaws *Corvus monedula* and depredation by Northern Goshawks *Accipiter gentilis*. Jackdaws were able to take over nest boxes from egg laying and incubating Tawny Owls, reducing the latter's breeding success. Tawny Owl numbers and breeding success were negatively correlated with Jackdaw numbers ($R^2 = 0.556$ and $R^2 = 0.592$, respectively). After the first nest in 1993, Goshawk numbers rapidly increased to 10–11 pairs in 1999. The number of Jackdaw breeding pairs correlated negatively with the number of Goshawks ($R^2 = 0.661$). Goshawks apparently limited Jackdaw numbers, which led to an improvement of Tawny Owl breeding success. However, post-fledging mortality of Tawny Owl from Goshawk predation was also significant, reducing local recruitment in the Tawny Owl breeding population.

Key words: nest-site competition, *Strix aluco*, *Accipiter gentilis*, *Corvus monedula*, intraguild predation

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INTRODUCTION

In the 1930s and 1950s, parts of the Amsterdam Water Supply Dunes (AWD) in the western Netherlands were afforested, initiating a substantial change in habitat structure with far-reaching consequences for the local bird population. In 1961–2007, we annually monitored the AWD for breeding raptors, owls, and corvids. This paper highlights the relationship between Tawny Owls *Strix aluco*, Jackdaws *Corvus monedula* and Northern Goshawks *Accipiter gentilis*. Linking the demography of species with habitat change, embedded in a long-term study, provides conservationists with an insight into the effects of management decisions.

METHODS

Study area and methods

The study area covers 3400 ha of coastal dunes in the western Netherlands, 20 km west of Amsterdam. The northern section encompasses 180 ha of open water in canals and infiltration beds, used for the production of drinking water. The western dunes are open with a herbaceous vegetation. The central parts are covered mainly with Sea Buckthorn *Hippophae rhamnoides*, interspaced with dune grasslands, thickets of birch *Betula* and hawthorn *Crataegus* and some small isolated pine *Pinus* plantations. In the first half of the 20th century, the eastern dunes were afforested with deciduous

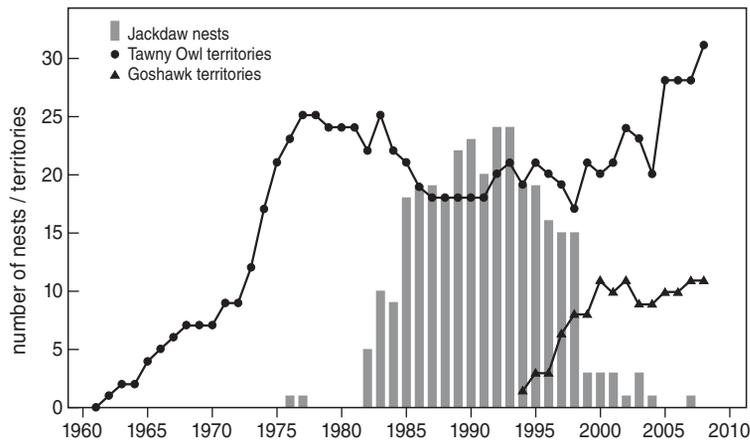


Figure 1. Trends of Tawny Owl (territories), Goshawk (territories) and Jackdaw (nests) in the AWD study area in 1961–2007.

and coniferous tree species, the larger part (560 ha) of which has since developed into mixed woods.

The study started in 1961, and continued up to and including 2007. Annually, we systematically surveyed the study area and mapped all territories of raptors and owls. By the time Tawny Owls started to colonize the dunes, natural cavities were scarce. Some owls bred on the ground, others in rabbit burrows. Starting in 1969, nest boxes were put up to be able to study the owls (and later: Jackdaws as well) more closely. The number of nest boxes gradually increased to 24 in 1975 and 38–40 from 1997 onwards. Annually, nest boxes and natural cavities were inspected for occupation by Tawny Owls and Jackdaws. Occupied nests were visited to gather information on clutch and brood size, and to ring the chicks. A pair was recorded as breeding when at least one egg had been laid; successful breeding was defined as a pair where at least one fledgling had been ringed and no remains were found in nest box or cavity after the breeding season. Nocturnal surveys were conducted during the post-fledgling period of Tawny Owls to locate overlooked pairs and to ring their chicks if possible. Adults were trapped and ringed during the breeding season and winter (starting in November) respectively from 1978 and 1981 onwards. We assume that we ringed all nestlings and adults belonging to the breeding population of the AWD. A non-ringed adult was therefore considered as originating from outside the study area. Recovery data on owls ringed as nestlings, and later found dead, were provided by the Dutch Centre for Avian Migration & Demography.

RESULTS

After an increase between 1961 and 1974, the Tawny Owl population stabilized at around 20–25 territories (Fig. 1). After the first nest of Goshawks was found in 1993, numbers increased rapidly up to 10–11 pairs in 1999 (Fig. 1). Although Jackdaws always had been present in the dunes, until 1981 very few pairs used the nest boxes provided for Tawny Owls (Fig. 1). From then on, Jackdaws increasingly took over nest boxes by dumping twigs upon the incubating owls (Buker & Hartog 1985, Koning 1986). This behaviour had an effect on the numbers of breeding Tawny Owls between 1981 until 1993 (Fig. 2). Jackdaw numbers correlated negatively with the number of territories occupied by Tawny Owls ($R^2 = 0.556$). This trend changed again from 1993 onwards, when Goshawks started to colonize the area and increased predation resulted in a decline in Jackdaw (Figs 1, 2), with a concomitant recovery of Tawny Owl numbers. The number of Goshawks correlated negatively with the number of Jackdaws ($R^2 = 0.661$).

Tawny Owls showed large annual variations in breeding success, but success was consistently lower during the period when Jackdaws were not yet facing the depredeations of Goshawks (Fig. 2). The breeding success of Tawny Owls correlated negatively with the number of Jackdaw nests ($R^2 = 0.592$, $P < 0.001$). From 1972 until 1982, 79% of Tawny Owl clutches ($n = 154$) produced one or more fledglings, declining to 46% ($n = 207$) between 1982 and 1998, then recovering to 71% between 1998 and 2007 ($n = 170$).

The proportion of adult female Tawny Owls recruited into the AWD breeding population was deter-

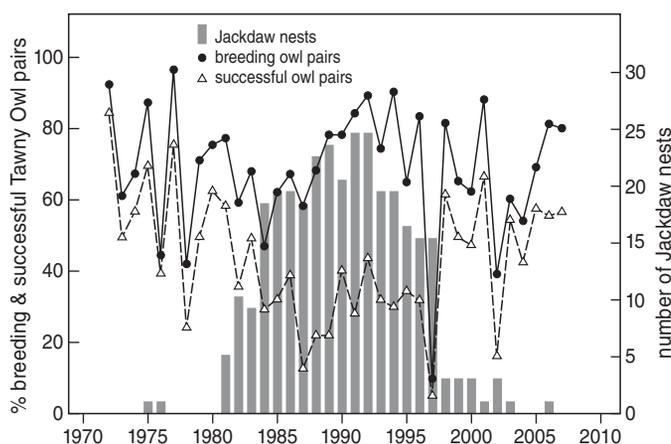


Figure 2. Breeding success of Tawny Owls in the AWD study area, but not the proportion of pairs breeding, dropped considerably in conjunction with the increase in Jackdaw numbers breeding in nest boxes, 1972–2007.

mined via the recapture of previously ringed owls. Changes in the number of ringed (i.e. local) vs. unringed (i.e. immigrated) Tawny Owls suggested that Goshawk predation on fledgling Tawny Owls had an impact on recruitment rates. Before 1989 the percentage of local recruits averaged $45.5\% \pm 2.5\%$ of the females; this proportion declined to $23.7\% \pm 1.3\%$ between 1992 and 2007.

DISCUSSION

In the 1960s Tawny Owls colonized the AWD and quickly grew to a density of 4.27 breeding pairs per 100 ha in the late 1970s and early 1980s. To study their reproductive behaviour, nest boxes were provided. These appeared attractive to owls, however other hole-breeding animals started using the boxes as well. Nestsite competition by Jackdaws resulted in far lower reproduction due to aggressive take-overs of Tawny Owl nests. Removal of this nest competitor by Goshawks allowed Tawny Owls to regain lost breeding opportunities and increase the number of successful pairs to pre-Jackdaw levels. However, the composition of the breeding population changed in favour of non-local recruits, probably because of an increase in post-fledging mortality caused by Goshawk predation.

Quantitative evidence for nest competition between Jackdaws and Tawny Owls has not previously been reported, but is well-known between Black Woodpeckers *Dryocopus martius* and Jackdaws (e.g. Johansson *et al.* 2008). Jackdaws have also been observed to use nest boxes specifically meant for Little

Owls *Athene noctua*, which led to the design of nest boxes that prevent Jackdaws from placing twigs in the entrance of the cavity (Van Nieuwenhuysse *et al.* 2008). Nest-related conflicts between cavity nesters are typical when cavities are in scarce supply. When cavities are not a scarce commodity, as for example in buildings in northeastern and southern Spain, breeding success of Lesser Kestrels *Falco naumanni* breeding alongside Rock Pigeons *Columba livia* and Jackdaws is similar to that of pairs breeding in single-species colonies (Forero *et al.* 1996).

Predation of medium-sized diurnal birds can be substantial after the colonization of forested areas by Goshawks. Eurasian Kestrels *Falco tinnunculus*, for example, showed a significant negative relationship with Goshawk numbers in northern England between 1975 and 1997 (Petty *et al.* 2003). Raptors in general accounted for 0–8% of prey numbers of Goshawks in 27 European studies, corvids even for 6–36% (Rutz *et al.* 2006). These findings are in agreement with data collected on the food of Goshawks in the AWD study area (Koning 1999). However, high levels of predation are not necessarily equivalent to declines in prey populations (Newton 1998, Rutz & Bijlsma 2006).

The main impact of Goshawks on Tawny Owls appears to be through predation of fledglings rather than adults (Petty & Thirgood 1989, Coles & Petty 1997, Petty *et al.* 2003, Sunde 2005). Fledgling Tawny Owls are particularly vulnerable because of their persistent begging calls (Petty *et al.* 2003), premature fledging and diurnal exposure (Sunde *et al.* 2003). Of 15 fledged owls that died of natural causes, 11 were killed by raptors, apparently all by Goshawks (Sunde *et*

al. 2003). Goshawks attempting to take fledglings may also elicit a defensive response from their parents, thus making them vulnerable too (Petty *et al.* 2003). The parents tend to trade off safety against the benefit of increased offspring survival through brood defense (Sunde *et al.* 2003). Diurnal avian predators, particularly Goshawks, appear to be the most prominent mortality agent for owls of all ages (Mikkola 1983), but this is probably biased (plucks of owls killed by predators are fairly easy to find). Alternatively, telemetry studies in Great Britain and Norway reported 48–79% mortality during the first two months after fledging, primarily due to starvation (Petty & Thirgood 1989, Coles & Petty 1997, Overskaug *et al.* 1999).

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SAMENVATTING

Een lange-termijn studie in de Amsterdamse Waterleidingduinen (1961-2007) volgde de ontwikkelingen van roofvogels en uilen op de voet. In deze voorheen open duingebieden werden in de jaren dertig en vijftig bossen aangeplant, die geleidelijk ook geschikt werden voor holenbewoners als Bosuilen *Strix aluco*. Door nestkasten te plaatsen ging het aantal potentiële broedplaatsen voor Bosuilen nog verder omhoog, totdat er – in de jaren tachtig en daarna – een overschot aan kasten beschikbaar was. Bosuilen namen in eerste instantie sterk in aantal toe, maar deze trend vlakke in de late jaren zeventig en vroege jaren tachtig af. De daaropvolgende afname werd veroorzaakt door Kauwen *Corvus monedula*, die in toenemende mate nestkasten overnamen en de Bosuilen verdreven. Aan deze ontwikkeling kwam een eind toen in 1993 de Havik *Accipiter gentilis* zich als broedvogel vestigde; zijn predatiedruk deed de stand van Kauwen kelderen. Dit leverde weer vestigingsmogelijkheden op voor Bosuilen, waarvan de stand zich herstelde tot het niveau van vóór de kauwenexplosie. De samenstelling van de broedpopulatie van Bosuilen is echter wel gewijzigd sinds de komst van Haviken. Door een hoge predatiedruk op pas uitgevlogen Bosuilen is het aandeel rekruten afkomstig uit de lokale broedpopulatie afgenomen, ten voordele van Bosuilen die buiten het studiegebied zijn geboren.

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