Identifying habitat sinks: a case study of Cooper's hawks in an urban environment

R. William Mannan · Robert J. Steidl · Clint W. Boal

Abstract We studied a population of Cooper's hawks (*Accipiter cooperii*) in Tucson, Arizona from 1994 to 2005. High rates of mortality of nestlings from an urban-related disease prompted speculation that the area represented an ecological trap and habitat sink for Cooper's hawks. In this paper, we used estimates of survival and productivity from 11 years of monitoring to develop an estimate of the rate of population change, λ, for Cooper's hawks in the area. We used a Cormack–Jolly–Seber approach to estimate survival of breeding hawks, and a stochastic, stage-based matrix to estimate λ. Despite the urban-related disease, the estimate of λ indicated that the area does not function as a habitat sink for Cooper's hawks ($\hat{\lambda}= 1.11 \pm 0.047$; $P = 0.0073$ for the null of $\lambda \leq 1$). Because data required to reliably identify habitat sinks are extensive and difficult to acquire, we suggest that the concept of habitat sinks be applied cautiously until substantiated with reliable empirical evidence.

Keywords Cooper's hawks · Demography · Ecological trap · Habitat sink · Lambda

Introduction

A "habitat sink" for a species is an area where productivity is insufficient to offset mortality (Pulliam 1988); thus, persistence of the population depends on emigrants from other areas and the annual rate of population change, λ, in the area is <1. Models of habitat selection suggest that dominant animals settle first in sites of highest quality and exclude other animals from those sites (Brown 1969; the despotic form of the Fretwell–Lucas Model, Fretwell and Lucas 1970). Once high quality sites are filled, offspring produced locally and

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individuals immigrating from elsewhere are forced to settle in sites of lesser quality. Sites settled last are lowest in quality and potentially function as habitat sinks (Pulliam and Danielson 1991).

Habitat sinks also may come into existence through "ecological traps," or circumstances where environmental cues related to habitat selection have become decoupled from habitat quality (reviews in Battin 2004; Robertson and Hutto 2006). Animals occupy areas that act as ecological traps because they perceive it as high quality habitat, but an event, organism, or situation to which the animal is not well adapted causes low reproduction, low adult survival, or both. Ecological traps may not result in population-level consequences (Robertson and Hutto 2006), but if the problem encountered by animals in the trap is severe and the resident population is not self-sustaining, the area by definition is a habitat sink (Donovan and Thompson 2001). Thus, some ecological traps are habitat sinks that are perceived as high quality habitat and preferred over other areas, rather than sites occupied as a last resort (Battin 2004; Gilroy and Sutherland 2007). Anthropogenic activities directly or indirectly cause most ecological traps (e.g., Mumme et al. 1999), therefore it seems likely that animals occupying urbanized environments, where human activities and alterations are in some circumstances ubiquitous, may be especially prone to situations that give rise to ecological trap and habitat sinks.

We studied a population of Cooper's hawks (*Accipiter cooperii*) in a metropolitan area from 1994 to 2005, and found evidence that the area provided high quality habitat for this species, including high nesting density (Boal and Mannan 1998), high rates of prey delivery to nestlings (Estes and Mannan 2003), high rates of adult survival (Boal 1997), and small home-range sizes during the breeding season (Mannan and Boal 2000). However, a disease (trichomoniasis) killed about 40% of offspring annually (Boal et al. 1998; Boal and Mannan 1999). Trichomoniasis is caused by a parasitic protozoan (*Trichomonas gallinae*), and in southeastern Arizona is associated with urban areas. Primary hosts of *T. gallinae* are members of the family Columbidae (Stabler 1954). In Tucson, doves are common and make up over half of the prey items delivered to nestling Cooper's hawks, but they constitute only 4% of the diet of Cooper's hawks in rural areas of southeastern Arizona (Estes and Mannan 2003). Differences in diet likely account for the differential rates of infection of trichomoniasis among nestling Cooper's hawks in Tucson (85% infected) and non-urban areas (9% infected; Boal et al. 1998), and lead to the high rate of nestling mortality in the urban area.

High mortality of nestlings from trichomoniasis prompted speculation that Tucson represented an ecological trap for Cooper's hawks (Boal and Mannan 1999; Battin 2004; Gilroy and Sutherland 2007). In this paper, we use information on productivity and survival of breeding hawks collected over 11years and estimates of survival from radio-tagged fledglings to estimate the annual rate of population change for Cooper's hawks in Tucson. Our objective was to determine whether Tucson is a habitat sink for Cooper's hawks, as would be indicated by λ being <1. We also discuss the empirical evidence necessary to identify habitat sinks reliably.

Methods

Study area

We studied Cooper's hawks in and near Tucson, Arizona, USA (32°N, 111°W), a metropolitan area that encompasses about 1,460km^2 with an estimated human population of

about 900,000 residents (Pima Association of Governments 2006). The city is comprised of a highly urbanized core surrounded by a mix of business complexes, relatively undeveloped areas (parks, golf courses), and high- and low-density residential areas. Tucson is located in the Sonoran Desert and supports remnants of lower and upper Sonoran vegetation communities and riparian corridors (Brown et al. 1979), although much of the natural vegetation has been removed or replaced with non-native plants.

Nest surveys

We located nests of Cooper's hawks during the breeding season (February–July) from 1994 to 2005 by searching historical nesting sites, areas where Cooper's hawks had been seen and reported to us by interested persons, sites from which injured nestlings or adults were collected by wildlife rehabilitators, and in groves of large trees (Boal and Mannan 1998). We visited nests at least once per week from the time they were found until the nestlings were between 15–20days of age or the nest failed. When nestlings were ≥15days old, we climbed nest trees and banded each nestling with a U.S. Geological Survey aluminum band. If nest trees were unsafe to climb, we waited until fledglings were beginning to hunt on their own (about 50days after hatching) in their natal area and attempted to capture them with bal-chatri traps (Bloom 1987). We banded captured fledglings and released them at the capture site. Sexual size dimorphism in Cooper's hawks is pronounced, with females being larger than males, including size of the tarsometatarsus (Hill 1944). We used diameter of the tarsometatarsus to distinguish male and female hawks (<5mm = males; ≥5mm = females). Based on observed behaviors (e.g., incubation, copulatory position), this method identified sex correctly in 99% of 92 hawks marked as nestlings or fledglings that eventually secured a breeding site in Tucson (Mannan et al. 2007).

We captured breeding hawks with bal-chatri or dho-gaza traps (Bloom 1987) and marked each hawk with a U.S. Geological Survey aluminum band on one leg, and a plastic, colored band on the other leg, etched with a unique alpha code. Letters on the plastic bands could be read from the ground with a 15–45× spotting scope or 20× binoculars. We attempted to re-sight marked hawks each year during nest visits. All field methods were approved by the University of Arizona Institutional Animal Care and Use Committee (Protocol 03-119).

Demography

We estimated nest success and described characteristics of successful broods, including brood size near fledging and sex ratio, from information collected while monitoring nests from 1994 to 2005. We used a Cormack–Jolly–Seber approach to estimate apparent survival of breeding hawks in Program MARK. We explored a set of ten candidate models to explain variation in survival. Candidate models were developed from combinations of a set of factors that had potential to explain variation in survival, including time (year), age, and sex. We used Akaike's Information Criteria to distinguish explanatory power of models.

We used estimates of first-year survival and nestling mortality from trichomoniasis that were reported previously (Boal 1997). First-year survival was estimated from the fates of hawks radio-tagged as fledglings in late summer (1999 and 2000) and monitored through early spring of the following year (Mannan et al. 2004); survival was estimated based on the Kaplan-Meier (1958) method. We used information from radio-tagged hawks to estimate first-year survival rather than from mark-recapture analysis of banded nestlings because mark-recapture analyses do not differentiate between emigration and death (Runge

et al. 2006), a limitation that can lead to underestimating survival, especially in the first year. Mortality from trichomoniasis was estimated from 1994 to 1996 (Boal 1997) and was based on counts of fledglings at about 40 days of age, when death from the disease abated. Although we did not consistently count fledglings between 1997 and 2005, trichomoniasis remained an agent of mortality throughout the study. We used the relatively high estimate of annual mortality from trichomoniasis (Boal 1997) in our model because it provided a conservative value with which to evaluate whether the area was a sink for Cooper's hawks. Because estimates of first year survival and mortality from trichomoniasis were from relatively short-term studies, they may not be representative of the entire study period.

We estimated the annual rate of population change, λ, with a stochastic, stage-based Leslie (Lefkovitch) matrix (McDonald and Caswell 1993) based only on demographic information from females. To estimate λ, we generated 10,000 matrices where each matrix element was chosen at random from distributions generated to match the sampling distributions of demographic parameters. We represented each parameter with either a normal distribution with mean equal to the empirical estimate and standard deviation equal to the estimated standard error or, for some parameters with binary outcomes, with a binomial distribution with mean equal to the empirically estimated proportion, based on a sample of 100. We determined λ based on the dominant eigenvalue for each matrix and generated a *P*-value for the null hypothesis that the population was stable or decreasing ($\lambda \leq$ 1) based on the ratio of values >1 (the alternative hypothesis) divided by the total number of matrices generated. We report all estimates ± 1 SE.

Results

From 1994 to 2005, we estimated nest success of Cooper's Hawks to be 84% based on outcomes of 637 nesting attempts, and size and sex ratio of broods near fledging from 413 successful nests (Table 1). Survival of juvenile hawks from hatching through 180 days was estimated to be 0.75 (SE = 0.15) for males and 0.64 (0.15) for females based on 527 relocations of 40 radio-tagged individuals (18 females and 22 males; Mannan et al. 2004).

Table 1 Estimates of demographic parameters used to estimate λ for Cooper's Hawks in Tucson, Arizona, 1994–2005

Parameter	Age class	*n*	Estimate	Standard Error
Survival of females	Adult, ≥2 years	161	0.813	0.0185
	Adult, 2 years	161	0.658	0.0681
	Juvenile	18	0.640[a]	0.150
Nest success (%)	Adult	577[b]	83.5	0.015
	Juvenile	60[b]	75.0	0.056
Brood size	Adult	371[c]	3.44	0.053
	Juvenile	42[c]	2.76	0.186
Female fledglings (%)	Juvenile	1,114[d]	47.3	0.015
Nestling mortality from trichomoniasis (%)	Juvenile	283[e]	41.0[f]	

[a] From Mannan et al. (2004)
[b] Number of nesting attempts
[c] Number of successful nests (i.e., those producing at least one fledgling)
[d] Number of nestlings near fledging
[e] Number of nestlings from 1994–1997
[f] From Boal (1997)

About half of the radio-tagged hawks ($n = 19$) were located sporadically throughout the fall and then disappeared. Trichomoniasis accounted for 80% of the mortality of nestling and fledgling Cooper's hawks recorded from 1994–1996 ($n = 144$), and killed about 40% of the offspring produced annually during that period (Boal 1997).

We estimated apparent survival of breeding hawks based on capture histories of 340 marked individuals, 161 females and 179 males (Table 1). Survival of breeding hawks was explained best with a model that included age-specific estimates of survival and constant detection probability $\{\phi_{age}, p.\}$; there were no competing models. In general, survival of adults was high, similar for males (0.80 ± 0.017) and females (0.80 ± 0.018), and did not vary annually across the study period. Survival in the second year of life for both male and female hawks combined, however, was lower (0.69 ± 0.055) than older birds (0.81 ± 0.013). Estimated detection probability was high and constant over time and among age and sex classes (0.93 ± 0.010). We estimated λ to be 1.11 ± 0.047 for Cooper's hawks in this urban area, with strong evidence that $\lambda > 1$ ($P = 0.0073$), indicative of an increasing population.

Discussion

Despite high mortality of nestlings from an urban-related disease, Tucson does not function as a habitat sink for Cooper's hawks. Our findings support the idea that urbanized landscapes can provide high quality habitat for some populations of Cooper's hawks (e.g., Rosenfield et al. 1996). We speculate that λ for the population we studied was >1 partly because of the relatively high annual rates of survival, especially of juvenile hawks. The estimate of juvenile survival we used in our model (0.64) could be biased high if most marked hawks not found during the radio-telemetry study died rather than emigrated (Mannan et al. 2004). This is unlikely, however, because 60% of juvenile hawks successfully tracked through winter were observed two or three years later when they first nested (Mannan et al. 2004), supporting our high estimate of survival for non-breeding Cooper's Hawks in Tucson. Furthermore, in the 2004 breeding season, 39% (32/82) of breeding males and 17% (14/82) of breeding females in the population were known to have been hatched in Tucson in previous years (Mannan et al. 2007). Because all nestlings in the population are not marked, this level of recruitment also adds support to relatively high survival rate of radio-marked juveniles we observed post-fledging.

The pattern of survival we observed among juvenile Cooper's hawks in this urban area differed from that commonly reported for predatory birds in more natural settings. For example, survival of predatory birds from fledging through their first winter of life, especially during dispersal, is low for many species (e.g., Belthoff and Richison 1989; Rohner and Hunter 1996; Ganey et al. 1998; but see Harmata et al. 1999). Availability of food, however, can influence survival of dispersing birds (e.g., Rohner and Hunter 1996). We speculate that high abundance of prey in Tucson (Estes and Mannan 2003; Mannan et al. 2004) may reduce mortality of Cooper's hawks during dispersal and throughout their first winter and compensate for the high, urban-related mortality incurred during the nestling period.

The concept of habitat sinks has been applied widely in current literature on population dynamics and has been used to explain a range of population processes, including interactions of populations in heterogeneous landscapes (e.g., Donovan et al. 1995; Zanette 2000; Murphy 2001), why introductions of exotic species often fail (Sax and Brown 2000), and micro-evolutionary consequences of moving nuisance animals from urban to rural areas

(Ashley et al. 2003). Further, the source-sink concept has been proposed as an appropriate foundation for conservation and restoration activities (e.g., Murphy 2001; Breininger and Oddy 2004). Despite widespread adoption of habitat sinks in the theoretical and applied literature, reliably documented sinks are uncommon, and the conditions under which they could persist remain controversial (Diffendorfer 1998).

Data required to reliably identify a habitat sink are extensive, and include estimates of productivity and survival over time periods that ideally encompass the range of environmental fluctuations that affect the species of interest. Based solely on these requirements, empirical evidence for habitat sinks should be rare, even if sinks are common in nature. In a review of source-sink population dynamics, only one study of a mobile animal (vesper sparrows [*Pooecetes gramineus*] nesting in agricultural fields; Rodenhouse and Best 2003) included sufficient data to reliably identify a habitat sink (Diffendorfer 1998). Most studies that claim evidence of a habitat sink lack sufficient demographic information, and even the vesper sparrow study used estimates of survival from other work (Diffendorfer 1998). Since that review, dozens of additional reports have speculated that areas under study might be functioning as habitat sinks (e.g., Ortega and Ortega 2003), but most lack sufficient data to reliably distinguish sinks from areas of low quality habitat where λ is approximately 1. Even the population of Cooper's hawks we studied has been suggested as a reliably documented sink (Battin 2004).

With few exceptions (e.g., Kreuzer and Huntly 2003; Breininger and Oddy 2004), most areas reliably identified as habitat sinks function as sinks because habitat quality has been reduced by anthropogenic causes (i.e., ecological traps). For example, territories of Florida scrub-jays (*Aphelocoma coerulescens*) along roads were classified as sinks because of high mortality of adults and young from collisions with automobiles (Mumme et al. 1999). Similarly, patches of habitat that function as sinks in "source-sink systems" often do so either through mortality associated directly with human activities (e.g., Reemes 2000; Harveson et al. 2004) or through mortality from predators and parasites whose numbers are excessive due to human activities (e.g., Budnik et al. 2001). Habitat sinks caused by ecological traps might be more common in urban areas than in more natural settings, but simply documenting high rates of mortality from an urban-related cause, as we did in our study, is insufficient evidence for a sink. We suggest that the concept of habitat sinks be applied cautiously until reliable evidence for their widespread existence becomes available.

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