Journal of Raptor Research

Advancing the science, conservation, and understanding of birds of prey

Journal of Raptor Research 60(1):jrr2514
doi: 10.3356/jrr2514

Irruptive Movements by Short-eared Owls and Concepts of Habitat Use: Commentary and Suggestions to Address Information Gaps

Joseph B. Buchanan,[1*] Robert A. Miller,[2] John Calladine,[3] and Travis L. Booms[4]

[1] *2112 Ravenna Lane SE, Olympia, WA 98501 USA*
[2] *Intermountain Bird Observatory, Boise State University, Boise, ID 83725 USA*
[3] *British Trust for Ornithology, Stirling, FK9 4NF, Scotland*
[4] *Alaska Department of Fish and Game, Fairbanks, AK 99701 USA*

KEY WORDS: *competition*; *habitat quality*; *habitat use*; *movements*; *nomadism*; *source-sink dynamics*.

The scope of strategies used by birds during seasonal movements is considerable and has been the subject of comprehensive syntheses (Bertold 2001, Newton 2024). The movements of species that employ irruptive or nomadic strategies are often unpredictable (Cottee-Jones et al. 2015), which can impede comprehensive understanding and subsequent implementation of effective conservation measures (Teitelbaum and Mueller 2019, Gibson et al. 2021). Across much of its extensive range, the Short-eared Owl (*Asio flammeus*) specializes on small mammal prey whose abundance varies or cycles markedly in both space and time. In response, the owls may travel thousands of kilometers between successive breeding areas to exploit localized prey abundances (Johnson et al. 2017, Calladine et al. 2024a). Research on this species has occurred across the northern hemisphere and elsewhere (Wiggins et al. 2020), and research and management priorities have been proposed (Booms et al. 2014). Here, we discuss aspects of Short-eared Owl colonization within the context of behavioral ecology and habitat selection, applying that framework to identify key questions that should be addressed in future research.

Short-eared Owls engage in irruptive or nomadic movements (for synthesis, see Newton 2024). In response to cyclic changes in small mammal prey abundance, the owls move across large landscapes, departing areas where prey abundance has crashed and settling in areas where prey resources are greater. These movements and the dynamics of predation represent a numerical response by the owls to a pulsed resource (e.g., Therrien et al. 2014). The changes in density of owls and their prey therefore shift through time and space (Newton 2024), as demonstrated for Short-eared Owls in several regions across the northern hemisphere (Village 1987, Korpimäki and Norrdahl 1991, Miller et al. 2023). In most cases (see potential exceptions, below), and acknowledging the uncertainties of site occupancy associated with nomadic birds (Teitelbaum and Mueller 2019, Calladine et al. 2024a, 2024b), the density of this species is likely a reliable indicator of habitat quality (but see Van Horne 1983). Assessing the specifics of source-sink dynamics is challenging due to the cost and effort required to generate demographic information needed to establish such relationships (Wiens and Van Horne 2011). However, it is logical that prey-rich locations are so different from prey-depleted locations that they likely function as sources to some extent (Pulliam 1988, Furrer and Pasinelli 2016).

Sources are commonly defined as areas where reproductive output exceeds mortality, whereas sinks are areas where mortality exceeds reproductive output (Pulliam 1988). By being more productive, sources are important to the population or subpopulation (as defined by Morrison et al. 2020) by enhancing lifetime reproductive success of individuals, resulting in greater recruitment of juveniles. In contrast, sinks require natal

---

* Corresponding author: jlrj@comcast.net

or breeding dispersal from sources to be maintained. Sources have traditionally been described as habitats or locations that are largely static or persistent (Pulliam 1988). In this manner, purported source areas used by Short-eared Owls differ in that they are ephemeral—functioning for only a segment of the small mammal prey cycle—and upon declining they lose much of their value and theoretically become sinks. Although emigration may imply the former source area had become a sink, it is also possible that a low density of owls may persist (Miller et al. 2023; and see Newton 2024). If owls' reproduction in those areas remains equal to or exceeds mortality, the area may not function as a sink per se.

Another aspect of assessing source-sink dynamics is related to how sources and sinks are defined. Pulliam (1988) did not include emigration as a demographic metric of source-sink dynamics (Runge et al. 2006). As a generality, including emigration success (e.g., survival and recruitment to the breeding population) might provide an informative assessment of sources by facilitating estimates of lifetime reproductive success. However, because Short-eared Owls can move great distances between successive breeding areas (Johnson et al. 2017, Calladine et al. 2024a), the relevance of emigration as a meaningful metric may be reduced if the probability of survival is inversely related to distance moved between breeding attempts.

A key part of the Fretwell-Lucas (ideal despotic distribution) theory of habitat selection is that early-arriving individuals use higher quality habitat, whereas later-arriving individuals occupy remaining areas, including those of lower quality (Fretwell and Lucas 1970). Consequently, according to the Fretwell-Lucas model, when Short-eared Owls first begin to settle in a region that is undergoing an increase in small mammal abundance, the first-arriving owls will occupy the best locations, and later arriving individuals settle in lower-quality areas. The Fretwell-Lucas model is logical for behavior of obligate migrants (i.e., birds that are hard-wired to migrate and that move in consistent ways) and Fretwell-Lucas may apply in certain cases for facultative migrants, those birds that exhibit irruptive movements only as needed to address changes in environmental conditions (Berthold 2001, Newton 2012). There is evidence that distances moved by Short-eared Owls outside of the breeding season could be density dependent (i.e., distances greater when densities are high; Calladine et al. 2012), and similar mechanisms could operate at other times with birds moving to more distant or lower quality habitats when numbers are high, which would be consistent with the ideal despotic distribution concept. A facultative migrant like the Short-eared Owl might move hundreds or thousands of kilometers between breeding areas from one year to the next (e.g., Johnson et al. 2017, Calladine et al. 2024a), and upon arriving at a new breeding area for the first time would have no prior knowledge of the quality of a landscape (Dale and Sonerud 2023). This could be particularly relevant for Short-eared Owls where survival rates can be quite low (e.g., mean annual survival rate of 0.47 reported in Europe), which implies that most individuals are unlikely to encounter good breeding opportunities (a vole outbreak) at the same place multiple times over their lifetime (Calladine et al. 2024a) and thus limits opportunities for individuals to acquire and use site-specific knowledge.

The manner of settlement by Short-eared Owls at a new landscape is likely influenced by local circumstances. One potential situation, as described above, is that first arrivals would claim the best areas, and later arrivals would occupy lesser areas in accordance with the Fretwell-Lucas model of the ideal despotic distribution. Alternatively, some high-quality landscapes may not be saturated by colonizing individuals (Newton 2006), which is a logical expectation given the lack of knowledge by owls of landscape conditions hundreds or thousands of kilometers from previous nesting areas (Dale and Sonerud 2023). In this case, a plausible situation is that later arriving individuals would also occupy high quality patches, because they were still available. Until the best habitat becomes saturated with owls, if that occurs, there is little or no competition.

In some situations, breeding Short-eared Owls occur in high local densities, resulting in aggregations that are considered semi-colonial (Arroyo and Bretagnolle 1999, Keyes et al. 2016). This raises the question about whether high-density areas reflect a numerical response to a superabundant food resource, if some other benefit of aggregation (e.g., reducing risk of predation; see Lockie 1955, Reid et al. 2011) influenced the behavior, or if the latter is simply an important byproduct of the former. Interactions may shift from interference competition to exploitative competition (Holdridge et al. 2016), and this might be anticipated during the transition from moderate or high prey densities to lower prey densities. If territory sizes were smaller during periods of high prey abundance (Village 1987) there would, in theory, be greater vigilance for predators but perhaps more competitive interactions (Lockie 1955, Pitelka et al. 1955). In contrast, during periods of fewer available prey resources, foraging areas might be larger (e.g., extending farther from nest sites), which might reduce vigilance and result in less competition for resources. Moreover, competition can alter growth rate in the local breeding cluster if conspecific interactions detract from breeding activities (Schoener 1973).

In subsequent years, yet another possibility is that the location of the best areas in the source landscape may have changed, from year one to year two, for example, as would be expected in the increasing phase of the small mammal prey cycle. Given such a change, owls from the previous year that remained in the landscape (or that returned from an overwintering area) may select new areas that are better than those of the previous year, which would indicate short-term philopatry to the landscape (i.e., they nested 2 yr in a row) although not to a specific territory. Because the increasing prey abundance continues to enhance the quality of the landscape, it would be expected that second-year arrivals might also encounter high-quality areas (including areas that were not high-quality locations in the first year), in the same manner as the first-year arrivals described above. It is also possible that at some point, the arrival of new individuals coupled with the output of reproduction from the high-quality landscape would result in competition for high-quality territories or in resource depletion (Newton 2006). This seems most likely to occur near or at the peak in the cycle of small mammal abundance, and certainly when prey abundance declines, causing local breeders and their offspring to search for more productive landscapes. Tracked Short-eared Owls have been recorded undertaking “loop movements” to areas 50 km or more from their occupied home range. Such flights may function to assess conditions in other areas, facilitating decisions to remain or settle elsewhere nearby (Calladine et al. 2024a; see Dale and Sonerud 2023).

The level of potential competition for resources (and the change in prey abundance) that occurs during both the increasing and decreasing phases of the prey cycle are largely unknown but may result in negative consequences of density-dependent habitat selection. This was documented in Snowy Owls (*Bubo scandiacus*) in eastern North America where immature owls used areas where they experienced higher levels of mortality (McCabe et al. 2022), suggesting the areas were ecological traps (Dwernychuk and Boag 1972, Battin 2004). With notable exceptions (e.g., Village 1987, Korpimäki and Norrdahl 1991), the uses of space by Short-eared Owls through time during the small mammal cycle are poorly understood in most areas. However, the occurrence of prey and the periodicity or magnitude of their cycles can change over time (e.g., Brommer et al. 2010) and space; for example, Short-eared Owls responded to a recently established subpopulation of voles by colonizing and breeding in Spain (Luque-Larena et al. 2013, Mougeot et al. 2022) and in the lower latitudes of North America, where small mammal prey cycles appear to be less pronounced (Miller et al. 2023). All such variations will influence the dynamics of how Short-eared Owls use space, but their “travel far, breed hard, and die young” life strategy appears adapted to take advantage of such spatially and temporally dynamic conditions (Dale and Sonerud 2023).

Relating Short-eared Owl movement to concepts of habitat selection and behavioral ecology may help focus future research. Of the following research questions, not all are mutually exclusive. Although most research on Short-eared Owls occurs in the northern hemisphere, the following questions may also be relevant in other parts of their range (Mikkola 2014, Enríquez 2017). (1) Assuming the existence of a source-sink dynamic, how long do source landscapes function as sources, and what is the temporal and spatial pattern of variation in habitat quality (e.g., source vs. sink), reproductive output, and subsequent survival and recruitment? (2) Do Short-eared Owls of source origin have a greater likelihood of survival than those from sinks or less productive locations, and does this influence survival rates for owls that travel great distances to new breeding areas? (3) Assuming there are differences among landscapes in the density of colonizing Short-eared Owls during the increasing part of the prey cycle, what factor(s) other than prey abundance (e.g., predators, human disturbance, prior experience at the site) distinguish between landscapes with differing densities of owls? (4) Do certain colonizing Short-eared Owls (e.g., recent recruits to the population) experience density-dependent influences in their use of habitat and potentially occupy areas that might function as ecological traps? (5) What is the threshold prey encounter or intake rate that triggers levels of competition through space and time, or the decision to remain or move? (6) Are there vigilance benefits associated with high densities of breeding Short-eared Owls, and as prey availability declines, do these benefits change? (7) Where there are differences in the magnitude of small mammal prey cycles across latitudes (e.g., less pronounced cycles at lower latitudes), do decisions to stay or disperse reflect local knowledge (e.g., staying at a known but marginally productive area at a lower latitude but departing from a similarly productive site farther north as a hedge bet that a higher quality area will be encountered)? (8) Due to the short life expectancy of Short-eared Owls (at least in some areas) and associated limited opportunities to acquire knowledge, are there differences in search behavior (e.g., at nearby versus distant locations) or other aspects of knowledge transference, including conspecific attraction?

Given the tremendous distances traveled by irruptive/nomadic species from one breeding location to another, sometimes in successive years, there is substantial uncertainty inherent in this movement strategy. The location of source or otherwise high-quality landscapes for Short-eared Owls varies through time in many regions, and the density of owls fluctuates in response to prey resources or competition. This uncertainty is consequently transferred to the conservation and management arena, illuminating the need for a better understanding of behavioral ecology and the variation in patterns of habitat use at multiple spatial and temporal scales across landscapes and regions (see Miller et al. 2023). Protecting specific places for the sake of irruptive/nomadic species may be ineffective because of the potential mismatch between place-based conservation and the movement ecology of irruptive species (Cottee-Jones et al. 2015). The questions we posed above should augment recommendations presented by Booms et al. (2014) and may enhance future research and subsequent development of conservation strategies for this and other irruptive/nomadic species.

We thank G. A. Sonerud and two anonymous reviewers for providing helpful comments that improved the manuscript.

LITERATURE CITED

Arroyo, B. E., and V. Bretagnolle (1999). Breeding biology of the Short-eared Owl (*Asio flammeus*) in agricultural habitats of southwestern France. Journal of Raptor Research 33:287–294.

Battin, J. (2004). When good animals love bad habitats: Ecological traps and the conservation of animal populations. Conservation Biology 18:1482–1491.

Bertold, P. (2001). Bird Migration: A General Survey. Oxford University Press, Oxford, UK.

Booms, T. L., G. L. Holroyd, M. A. Gahbauer, H. E. Trefry, D. A. Wiggins, D. W. Holt, J. A. Johnson, S. B. Lewis, M. D. Larson, K. L. Keyes, and S. Swengel (2014). Assessing the status and conservation priorities of the Short-eared Owl in North America. Journal of Wildlife Management 78:772–778.

Brommer J. E., H. Pietianen, K. Ahola, P. Karell, T. Karstinen, and H. Kolunen (2010). The return of the vole cycle in southern Finland refutes the generality of the loss of cycles through "climatic forcing." Global Change Biology 16:577–586.

Calladine, J., C. du Feu, and R. du Feu (2012). Changing migration patterns of the Short-eared Owl *Asio flammeus* in Europe: An analysis of ringing recoveries. Journal of Ornithology 153:691–698.

Calladine, J., G. T. Hallgrimsson, N. Morrison, C. Southall, H. Gunnarsson, F. Jubete, F. Sergio, and F. Mougeot (2024a). Remote tracking unveils intercontinental movements of nomadic Short-eared Owls (*Asio flammeus*) with implications for resource tracking by irruptive specialist predators. Ibis 166:896–908.

Calladine, J., C. Southall, A. Wetherhill, and N. Morrison (2024b). Use of dwarf shrubland-grassland mosaics by a nomadic predatory bird: The Short-eared Owl *Asio flammeus*. Journal of Ornithology 165:1039–1049.

Cottee-Jones, H. E. W., T. J. Matthews, and R. J. Whittaker (2015). The movement shortfall in bird conservation: Accounting for nomadic, dispersive and eruptive species. Animal Conservation 19:227–234.

Dale, S., and G. A. Sonerud (2023). Hawk owl irruptions: Spatial and temporal variation in rodent abundance drive push and pull dynamics. Oecologia 201:31–43.

Dwernychuk, L. W., and D. A. Boag (1972). Ducks nesting in association with gulls – an ecological trap? Canadian Journal of Zoology 50:559–563.

Enríquez, P. L. (Editor) (2017). Neotropical Owls: Diversity and Conservation. Springer International Publishing, Cham, Switzerland.

Fretwell, S. D., and H. L. Lucas (1970). On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoretica 19:16–36.

Furrer, R. D., and G. Pasinelli (2016). Empirical evidence of source-sink populations: A review of occurrence, assessments and implications. Biological Reviews 91: 782–795.

Gibson, M. R., C. A. Runge, P. A. Stephens, R. A. Fuller, and S. G. Willis (2021). Where nothing stands still: Quantifying nomadism in Australian arid-zone birds. Landscape Ecology 37:191–208.

Holdridge, E. M., C. Cuellar-Gempeler, and C. P. terHorst (2016). A shift from exploitation to interference competition with increasing density affects population and community dynamics. Ecology and Evolution 6:5333–5341.

Johnson, J. A., T. L. Booms, L. H. DeCicco, and D. C. Douglas (2017). Seasonal movements of the Short-eared Owl (*Asio flammeus*) in western North America as revealed by satellite telemetry. Journal of Raptor Research 51:115–128. doi:10.3356/JRR-15-81.1.

Keyes, K. L., M. A. Gahbauer, and D. M. Bird (2016). Aspects of the breeding ecology of Short-eared Owls (*Asio flammeus*) on Amherst and Wolf Islands, eastern Ontario. Journal of Raptor Research 50:121–124. doi: 10.3356/rapt-50-01-121-124.1.

Korpimäki, E., and K. Norrdahl (1991). Numerical and functional responses of kestrels, Short-eared Owls, and Long-eared Owls to vole densities. Ecology 72:814–826.

Lockie, J. D. (1955). The breeding habits and food of Short-eared Owls after a vole plague. Bird Study 2:63–69.

Luque-Larena, J. J., F. Mougeot, J. Viñuela, D. Jareño, L. Arroyo, X. Lambin, and B. E. Arroyo (2013). Large-scale range expansion and outbreaks of common vole (*Microtus arvalis*) in agricultural plains of NW Spain. Basic and Applied Ecology 14:432–441.

McCabe, R. A., J.-F. Therrien, K. Wiebe, G. Gauthier, D. Brinker, S. Weidensaul, D. Reid, F. I. Doyle, K.-O. Jacobsen, T. Aarvak, I. J. Øien, et al. (2022). Density-dependent winter survival of immatures in an irruptive raptor with pulsed breeding. Oecologia 198:295–306.

Mikkola, H. (2014). Owls of the World: A Photographic Guide. Second Ed. Firefly Books, Buffalo, NY, USA.

Miller, R. A, J. D. Carlisle, C. Moulton, T. L. Booms, T. L. Pope, and J. B. Buchanan (2023). Temporal and spatial population dynamics of the nomadic Short-eared Owl across the western United States. Journal of Wildlife Management 87:e22369. doi:10.1002/jwmg.22369.

Morrison, M. L., L. A. Brennan, B. G. Marcot, W. M. Block, and K. S. McKelvey (2020). Foundations for Advancing Animal Ecology. Johns Hopkins University Press, Baltimore, MD, USA.

Mougeot, F., F. Jubete, and A. Onrubia (2022). Búho campestre *Asio flammeus*. In III Atlas de las Aves en Época de Reproducción en España (B. Molina, A. Nebreda, A. R. Muñoz, J. Seoane, R. Real, J. Bustamante and J. C. del Moral, Editors). SEO/BirdLife, Madrid, Spain. https://atlasaves.seo.org/ave/buho-campestre/.

Newton, I. (2006). Advances in the study of irruptive migration. Ardea 94:432–460.

Newton, I. (2012). Obligate and facultative migration in birds: Ecological aspects. Journal of Ornithology 153(Suppl. 1):S171–S180.

Newton, I. (2024). The Migration Ecology of Birds. Academic Press, London, UK.

Pitelka, F. A., P. Q. Tomich, and G. W. Treichel (1955). Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. Ecological Monographs 25:85–117.

Pulliam, H. R. (1988). Sources, sinks, and population regulation. American Naturalist 132:652–661.

Reid, D. G., F. I. Doyle, A. J. Kenney, and C. J. Krebs (2011). Some observations of Short-eared Owls, *Asio flammeus*, ecology on Arctic tundra, Yukon, Canada. Canadian Field-Naturalist 125:307–315.

Runge, J. P., M. C. Runge, and J. D. Nichols (2006). The role of local populations within a landscape context: Defining and classifying sources and sinks. American Naturalist 167:925–938.

Schoener, T. W. (1973). Population growth regulated by intraspecific competition for energy or time: Some simple representations. Theoretical Population Biology 4: 56–84.

Teitelbaum, C. S., and T. Mueller (2019). Beyond migration: Causes and consequences of nomadic animal movements. Trends in Ecology and Evolution 34:569–581.

Therrien, J.-F., G. Gauthier, D. Pinaud, and J. Bêty (2014). Irruptive movements and breeding dispersal of Snowy Owls: A specialized predator exploiting a pulsed resource. Journal of Avian Biology 45:536–544.

Van Horne, B. (1983). Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47: 893–901.

Village, A. (1987). Numbers, territory size and turnover of Short-eared Owls *Asio flammeus* in relation to vole abundance. Ornis Scandinavica 18:198–204.

Wiens, J. A., and B. Van Horne (2011). Sources and sinks: What is the reality? In Sources, Sinks and Sustainability (J. Liu, V. Hull, A. T. Morzillo, and J. A. Wiens, Editors). Cambridge University Press, New York, NY, USA. pp. 507–519.

Wiggins, D. A., D. W. Holt, and S. M. Leasure (2020). Short-eared Owl (*Asio flammeus*). In Birds of the World (S. M. Billerman, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. doi:10.2173/bow.sheowl.01.

Received 30 January 2025; accepted 5 June 2025