

SEASONAL AND SEX-BIASED SURVIVAL OF ADULT INTERIOR WESTERN SCREECH-OWLS (*MEGASCOPS KENNICOTTII MACFARLANEI*) IN SOUTHEAST BRITISH COLUMBIA

DORIS HAUSLEITNER

Seepanee Ecological Consulting, 2880 Granite Road, Nelson, BC V1L 6Y5 Canada; Selkirk College, 301 Frank Beinder Way, Castlegar, BC V1N 4L3 Canada; dorishaus@shaw.ca

JAKOB DULISSE

Jakob Dulisse Consulting, 410 Second Street, Nelson, British Columbia V1L 2L3, Canada

IRENE MANLEY

Ministry of Forests, Lands and Natural Resource Operations, 401-333 Victoria Street, Nelson, BC V1L 4K3 Canada

ABSTRACT—In Canada and in British Columbia, the interior Western Screech-Owl (*Megascops kennicottii macfarlanei*) has been assessed as a species at risk primarily as a result of loss and degradation of low-elevation riparian habitat. Few data exist on population demographics of this subspecies. We analyzed annual survival of 19 radio-tagged adult owls from 2009 through 2013 using known-fate models. Time and sex dependence in annual survival rates were examined. The best approximating models suggested that female annual survival (28%) was lower than male survival (83%). Owl survival was lowest prior to incubation and during brood rearing, times when owls are most vocal. Mortality was attributed to avian predation and road mortality. Management practices to preserve habitat during the critical breeding period are encouraged in light of this research.

Key words: British Columbia, known-fate models, *Megascops kennicottii macfarlanei*, radio-telemetry, sex-specific, survival, Western Screech-Owl

In British Columbia, 2 subspecies of Western Screech-Owl are recognized: the interior (*Megascops kennicottii macfarlanei*) and coastal subspecies (*M. k. kennicottii*). *M. k. macfarlanei* is distributed in the southern interior of British Columbia and ranges from the community of Lillooet to the west and the Flathead Valley to the east (Fig. 1; COSEWIC 2012). This subspecies was recently assessed federally as threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2012) and the Species at Risk Act. Provincially, it is red-listed (BCCDC 2014) and is managed under the Identified Wildlife Management Strategy (MWLAP 2004). Population declines are primarily attributed to low-elevation habitat loss and degradation (COSEWIC 2012).

Western Screech-Owls are socially monogamous and retain mates for life (Hertling and Belthoff 2001). They are sexually dimorphic,

with females averaging 4% larger than males (Cannings and Angell 2001). Western Screech-Owls are territorial and remain on territories in low-elevation riparian forests year-round (Davis and Weir 2010). They typically nest in mature Black Cottonwood (*Populus trichocarpa*) trees (Cannings and others 1987) and roost and forage in adjacent coniferous habitat and meadows (Cannings and Davis 2007). Eastern Screech-Owl (*Megascops asio*) males defend nests more vigorously than females (Sproat and Ritchison 1993), and Western Screech-Owl males supply most of the food during the nestling period (Cannings and Angell 2001), so we hypothesised that male survival would be lower than that of females.

Reproduction and survival are essential components of animal fitness and population dynamics (Byron and others 2001). Estimates for reproduction are generally easier to measure

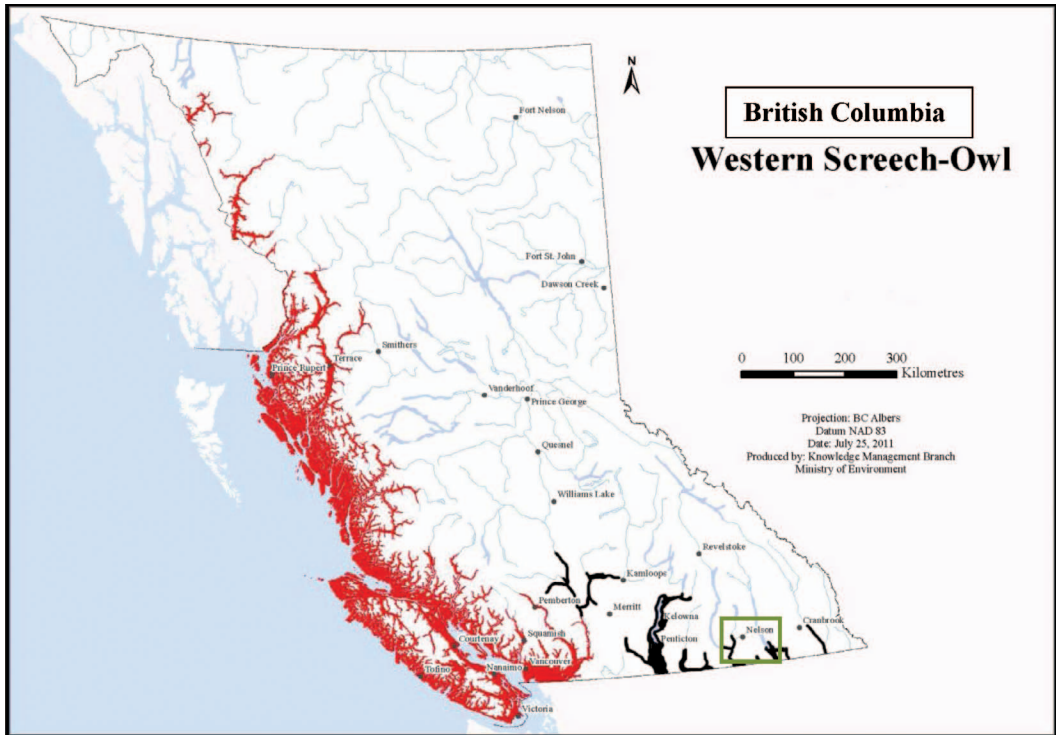


FIGURE 1. Distribution of Western Screech-Owls, coastal *kennicottii* sub-species in red, and the interior *macfarlanei* in black. Study area is outlined in green. Map adapted from COSEWIC (2012).

than survival, as the latter require long-term studies of marked individuals (Lebreton and others 1992). For endangered species, survival rates are critical to monitor populations and in designing conservation plans (Lebreton and others 1992). Relatively little is known about Western Screech-Owl demographic parameters (Cannings and Angell 2001); research on survival and mortality sources has been recommended for the species' recovery in Canada (WSRT 2008).

METHODS

We attempted to capture owls after locating them by call playback inventory (concurrent study) during a time when they were most territorial (March–July and September, 2009–2012). Captures took place at 12 territories located in southeastern British Columbia within the Southern and Central Columbia Mountains and Southern Purcell Mountains ecozones (Demarchi 1995), and included the low-elevation (<1000 m) areas near Creston, Salmo, Slocan, Trail, and Fruitvale (Fig. 1). These areas

are within the Interior Cedar Hemlock biogeoclimatic zone (ICHxw, ICHdw1 variants; BCMOF 2004). The regional forest ecosystem is diverse and main tree species include Douglas-fir (*Pseudotsuga menziesii*), Western Hemlock (*Tsuga heterophylla*), Lodgepole Pine (*Pinus contorta*), Western Redcedar (*Thuja plicata*), Grand Fir (*Abies grandis*), Paperbirch (*Betula papyrifera*), Ponderosa Pine (*Pinus ponderosa*), Trembling Aspen (*Populus tremuloides*), and Black Cottonwood (*Populus trichocarpa*). Common Snowberry (*Symphoricarpos albus*), Beaked Hazelnut (*Corylus cornuta*), Chokecherry (*Prunus virginiana*), Tall Oregon Grape (*Mahonia aquifolium*), False-box (*Paxistima myrsinites*), Saskatoon (*Amelanchier alnifolia*), Red-osier Dogwood, (*Cornus stolonifera*), Thimbleberry (*Rubus parviflorus*), and Douglas Maple (*Acer glabrum*) are common shrubs.

For capture, we set up a 9 x 3 m, 60-mm mesh mist net with a Western Screech-Owl stuffed decoy mounted on a 1.5-m meter pole adjacent to the net. Using a megaphone (model ER-604W, TOA Corporation, Kobe, Japan) below

the decoy and approximately at the center of the net, we broadcast a variety of social and mating calls (Smith and others 1983) recorded from owls in the Okanagan region of British Columbia. Call playback, controlled via a long cord connected to an MP3 player (model a1236 EMC iPod, Apple Inc, Cupertino, California, USA), commenced approximately 1 h after sunset, was played for 1.5 min, and followed by 3.5 min of silence between cycles. To minimize disturbance to owls, we limited our capture attempts to 1-h sessions per night and only attempted captures at the same territory for 2 subsequent nights. If a Barred Owl (*Strix varia*) or Great Horned Owl (*Bubo virginianus*) was seen or heard, we ceased capture attempts for that night. We used fishing bells attached to the net to alert observers when owls struck the net. We used a bal-chatri trap baited with a live domestic mouse in tandem with the mist nets for 11 of 19 owl captures. If an owl showed interest in the prey, we stopped broadcasting and allowed the owl to focus solely on the prey. Nets and traps were attended at all times.

Individuals were classified according to sex using a combination of morphological measurements (mass, wing chord) and by analysing their vocalizations during and after capture. The male call is lower in frequency than that of the female (Hertling and Belthoff 2001) and can be identified by ear especially when both sexes are calling. Owls were banded and radio-tagged with backpack-mounted transmitters as described by Smith and Gilbert (1981; model no. PD-2 and RI-2C, Holohil Systems, Carp, Ontario, Canada). Radios were sewn and glued in place using epoxy. Transmitters weighed 3.7 to 6.0 g ($\leq 3.0\%$ of the mass of the birds), had a 20-cm antennae, and a battery lifespan range of 6 to 9 mo.

Owls were directly tracked using an H-antenna and Lotek STR 1000 receiver once per week and their presence visually confirmed on roosts. No call playbacks were used during telemetry. We tried to determine cause of death from carcasses and associated sign at a kill site as soon as possible after time of death, recognizing that scavengers can make it difficult to assess cause-specific mortality (Bumann and Stauffer 2002). Mortality events were classified as avian predation if feathers were plucked without evidence of chewing, roosting owls or raptors were found nearby, pellet or whitewash was

TABLE 1. Annual survival models varying by sex, year, month, and season for *M. k. macfarlanei* in southeast British Columbia, 2009–2013. K is the number of parameters estimated by the model; Dev is deviation; Δ AICc is the difference between a given model and the model with the lowest AICc¹ score; and AICc weight (w_i) reflects the relative support for each model.

Model	K	Dev	Δ AICc	w_i
S (sex)	2	49.2	0.0	0.43
S (season)	3	49.0	1.9	0.18
S (season * sex)	6	42.5	1.9	0.18
S (null model)	1	54.1	2.8	0.11
S (year)	2	54.0	4.9	0.04
S (year + month)	7	45.0	6.7	0.02
S (year)	2	54.0	4.9	0.03

¹ The lowest AICc score was 53.3.

found at the site, or no bite marks were found on the transmitter. As radios were sewn and glued in place during capture, we knew an owl was predated if the transmitter was recovered on its own with straps intact. In these cases, however, there was not enough evidence to determine cause of mortality ($n = 3$).

We analyzed annual survival in program MARK (White and Burnham 1999), using known-fate models which incorporate the Kaplan-Meier product-limit method (Kaplan and Meir 1958) with staggered entry (Pollock and others 1989). Known-fate models assume radio tagging does not affect an individual's fate, individual fates are independent, and that censoring is unrelated to mortality (White and Burnham 1999). We had no deaths in the 1st week immediately following capture, and 4 individuals that were recaptured gained weight while wearing a transmitter. We constructed models with sex as a group effect and year as a covariate to determine whether survival rates varied by year, month, season, or sex or a combination of these variables. Two owls were recaptured and radios replaced for a subsequent year of study, yielding 2 y of survival data. Annual survival was estimated for the year starting March 1. Seasons were delineated as breeding-nesting (February–April), rearing young (May–August), and non-breeding (September–January). We based model selection on the small-sample size adjusted Akaike's information criterion (AICc). Models within a Δ AICc < 2 showed insufficient evidence to be excluded as the most credible models. A Δ AICc > 2 but < 4 provided weak evidence that

TABLE 2. Estimated male ($n = 9$), female ($n = 10$), and total (S) seasonal survival rates of *M. k. macfarlanei* in southeast British Columbia, 2009–2013, reported as % \pm SE. Seasons were delineated as breeding-nesting (February–April), rearing young (May–August), and winter (September–January).

Season	Male	Female	Total S
breeding-nesting	100 \pm 0.0	70.0 \pm 14.5	84.2 \pm 8.4
rearing young	95.7 \pm 4.3	91.3 \pm 5.9	93.5 \pm 3.6
winter	100 \pm 0.0	96.1 \pm 3.8	98.4 \pm 1.6

the models were not the best fitted in the set. Models with Δ AICc > 4 but < 7 exhibited strong evidence that the models were not the best fit in the set for the data (Burnham and Anderson 1998). Results reported are estimates \pm SE.

RESULTS

We captured and radio tagged a total of 17 unique adult *M. k. macfarlanei* from 12 territories between 2009 and 2012. From these owls we obtained 692 radio locations between March 2009 and February 2013. The models that best fit the data for annual survival were those in which survival varied between sexes and amongst seasons and years (Table 1). Apparent annual survival (ϕ) for all adult owls was 63.2%, whereas annual survival probability (S) was 50.4% \pm 13.1 ($n = 19$). Male and female survival probabilities were 83.4% \pm 15.1 ($n = 9$) and 27.6% \pm 14.5 ($n = 10$), respectively. Seasonal survival was lowest for females ($S = 70.0\% \pm 14.5$) during breeding-nesting, and lowest for males during brood rearing (Table 2).

Seven owls died during the study, of which 6 were female (Table 3). For 3 individuals, only the radio remained and their cause of death could not be determined (Table 3). Three individuals died of avian predation during breeding and brood rearing. The remains of one of these females were found at the top of a broken-top tree and we suspect that she was killed by a Northern Goshawk (*Accipiter gentilis*). One was killed by a Barred Owl and the other was killed by either a Barred or Great Horned Owl. One female was recovered after being hit by a car on a busy road.

DISCUSSION

Our overall average estimate of annual survival was 50%, with 83% and 28% survival of males and female, respectively. Although no

TABLE 3. Cause-specific mortality of *M. k. macfarlanei* by sex, month, and year in southeast British Columbia, 2009–2013.

Sex	Year	Month of death	Likely cause of mortality
M	2009	June	Great Horned-Barred Owl
F	2009	July	Unknown
F	2010	February	Unknown
F	2010	March	Barred Owl
F	2011	August	Goshawk
F	2012	February	Unknown
F	2012	October	Vehicle

other estimates of survival exist that we know of, other studies in British Columbia have reported high territory turn-over rates (Tripp and Otter 2006; Davis and Weir 2008). In the Shuswap region of British Columbia, there was a higher estimated territory turnover rate for radio-tagged *M. k. macfarlanei* females (71%; $n = 7$) than for males (66%; $n = 6$) (Davis and Weir 2008). Based on vocal analysis of *M. k. kennicottii*, territory turn-over rates on Northern Vancouver Island were estimated as 28–50% (Tripp and Otter 2006).

Female *M. k. macfarlanei* survival was considerably lower than that of males, consistent with other studies showing female-biased avian mortality across 194 bird species (Liker and Székely 2005). Perhaps for female *M. k. macfarlanei*, energetics for egg production, incubation, and brooding may have a higher cost on survival than male nest and territorial defense and feeding. As Western Screech-Owls are socially monogamous, less intense male-male competition is required. Additionally, only 2 territories in the study area occurred adjacent to each other, so the energetics required for male intraspecific defense was likely low.

However, studies of Northern Spotted Owls (*Strix occidentalis caurina*; Forsman and others 2011), and Tawny Owls (*Strix aluco*; Karell and others 2009) showed no sex differences in adult annual survival. Millon and others (2010) showed adult survival (age ≥ 2) in Tawny Owls to be higher for females than males. Similarly, Severinghaus and Rothery (2008) reported female survival of Lanyu Scops Owls (*Otus elegans botelensis*) to be consistently higher (7%) than that of males.

Social monogamy generally produces male-biased ratios (Brotherton and Komers 2003). Given the small population size of *M. k.*

macfarlanei in the west Kootenay region, large variation in survival by sex can have profound effects on population dynamics and extinction probabilities, and must be considered in conservation planning (Magdalena and others 2011).

In addition to sex, the models that best described the data included survival varying with season. Owl mortalities coincided with seasons when the species was most vocal; during breeding and nesting (late February and March, $n = 3$), and again during brood rearing (June, July, and August, $n = 3$). The number and duration of vocalizations is greatest during the breeding season (Hertling and Belthoff 1997). *M. k. macfarlanei* began unsolicited calling in the west Kootenay region from mid-February to the end of March prior to nest initiation. Earliest nest initiation in the west Kootenay region was March 15 ($n = 7$). Similarly, most of the territory turnover observed in the Shuswap occurred during February and March (Davis and Weir 2008). Owls are relatively quiet through nesting (Cannings and Angell 2001); however, broods followed through radio tagging were quite conspicuous once young fledged and before they dispersed, mostly because juvenile birds maintained constant vocal contact with parents. Fledging in the west Kootenay region occurred from the last week of May through mid-June ($n = 11$). Dispersal of juvenile owls occurred approximately 8 wk post-fledging. All 3 owls (2 females, 1 male) killed in June, July, and August had fledglings with them at the time of their mortality. We also documented juvenile mortality during this time period, as 1 of 4 radio-tagged juvenile owls died of predation before dispersing.

Three mortalities were likely due to avian predation, and occurred at times when owls are most conspicuous. Evidence suggests that 2 mortalities of adult *M. k. macfarlanei* can be attributed to Barred or Great Horned Owls. Similarly, the Shuswap radio-telemetry study attributed 2 of 3 mortalities of radio-tagged adults to predatory owls (Barred or Great Horned; Davis and Weir 2008). Barred Owls were observed during capture attempts and flew in silently several times during inventory. A male from a territory with particularly aggressive Barred Owls, shifted to an adjacent territory when his mate died. Barred Owl expansion in coastal North America appears to coincide with Western Screech-Owl declines

(Elliot 2006; Acker 2012). The impact that Barred Owls have on Western Screech-Owl populations has not yet been quantified, but will likely increase in the coming years as Barred Owls become more established (Acker 2012).

One radio-tagged individual died of road mortality, and 2 untagged *M. k. macfarlanei* were found killed on roads in the Kootenays during our study. Similarly, a radio-tagged individual and an unmarked individual were killed along roads in the Shuswap region (Davis and Weir 2008). From 1995 to 2005, 16 *M. k. kennicottii* were found killed by vehicle traffic in the Lower Mainland and Central Fraser Valley (Preston and Powers 2006). Road mortality is likely associated with both subspecies' use of edge habitat, and is likely to increase with further development of riparian areas. Current management of *M. k. macfarlanei* on public lands in British Columbia include the creation of Wildlife Habitat Areas (WHAs), which conserve breeding habitat. Under this strategy, it is recommended that road building is avoided within a WHA (MWLAP 2004); our research supports this recommendation.

In owl species, reproductive performance (Flesch and Steidl 2010) and survival can vary with habitat quality (Drugger and others 2005; Hakkarainen and others 2007). Conserving breeding habitat on public lands (WHAs) is encouraged in light of our research, which suggests that mortality is highest for *M. k. macfarlanei* during the breeding period. Wildlife habitat areas should reflect current knowledge about home-range sizes in British Columbia (Davis and Weir 2010). On private lands, stewardship practices and land acquisition should focus on habitat use during the critical breeding period.

ACKNOWLEDGEMENTS

These research activities were completed with financial support from Fish and Wildlife Compensation Program-Columbia, Columbia Basin Trust, Habitat Conservation Trust Fund, Habitat Stewardship Program, and FortisBC. Thank you to J Krebs, T Oussoren, A Glass, and B Woodbridge from the Fish and Wildlife Compensation Program. Many thanks go to A Waterhouse and K McGuinness for GIS analysis. We wish to thank the Creston Valley Wildlife Management Area for access and permits. Thank you to R Cannings for guidance in capture. Thanks to T Antifeau and O Dyer from the BC Ministry of Environment for support. A big thanks to H Davis and R Weir for answering countless questions, providing guidance and capture equipment.

Thank you to T Tripp for providing vocalizations used in call playback surveys. Thanks to L Zsoldos and K Syvchuck for field assistance. Thank you also to field assistance from T, M, and D Abraham, T Cooper, A Glass, T Hill, M-A Beaucher, M Mailhot, G Mowat, R Irvine, A McMillan, B Huw, V Shaw, A Kortello, C Aylmer, J Wallace, K Dulisse, S Fassina and C Swanson. Thank you to A and A Hausleitner for generous hospitality and accommodations in Creston. The biggest thanks go to all landowners, some of who tipped us off about Screech-Owls on their properties, and for allowing us access to their lands.

LITERATURE CITED

- ACKER J. 2012. Recent trends in Western Screech-Owl and Barred Owl abundances on Bainbridge Island, Washington. *Northwestern Naturalist* 93:133–137.
- [BCCDC] BRITISH COLUMBIA CONSERVATION DATA CENTRE. 2014. BC Species and Ecosystems Explorer. Ministry of Environment, Victoria, BC. <http://a100.gov.bc.ca/pub/eswp>. Accessed 24 July 2014.
- [BCMOF] BRITISH COLUMBIA MINISTRY OF FORESTS 2004. Biogeoclimatic zones of British Columbia. 1:250,000 digital data. Province of British Columbia, Victoria, BC, Canada.
- BROTHERTON PNM, KOMERS PE. 2003. Mate guarding and the evolution of social monogamy in mammals. In: Reichard UH, Boesch C, editors. *Monogamy: Mating strategies and partnerships in birds, humans and other mammals*. Cambridge, UK: Cambridge University Press. p 42–58.
- BUMANN GB, STAUFFER DF. 2002. Scavenging of ruffed grouse in the Appalachians: influence and implications. *Wildlife Society Bulletin* 30:853–860.
- BURNHAM KP, ANDERSON DR. 1998. Model selection and multimodel inference: A practical information theoretic approach, second edition. New York, NY: Springer-Verlag. 488 p.
- BYRON KW, NICOLS JD, CONROY MJ. 2001. Analysis and management of animal populations. Modeling, estimation and decision making. San Diego, CA: Academic Press. 817 p.
- CANNINGS RJ, ANGELL T. 2001. Western Screech-Owl (*Otus kennicottii*). In: Poole A, Gill F, editors. *The birds of North America*, 597. Philadelphia, PA: Academy of Natural Sciences and Washington DC: American Ornithologists' Union. 20 p.
- CANNINGS RJ, DAVIS H. 2007. Status of the Western Screech-Owl *macfarlanei* subspecies (*Megascops kennicottii macfarlanei*) in British Columbia. Victoria, BC: BC Ministry of Environment. Wildlife working report No. WR-112.
- CANNINGS RA, CANNINGS RJ, CANNINGS SG. 1987. Birds of the Okanagan Valley, British Columbia. Victoria, BC: Royal British Columbia Museum. 420 p.
- [COSEWIC] COMMITTEE ON THE STATUS OF ENDANGERED WILDLIFE IN CANADA. 2012. COSEWIC assessment and status report on the Western Screech-Owl *kennicottii* subspecies *Megascops kennicottii kennicottii* and the Western Screech-Owl *macfarlanei* subspecies *Megascops kennicottii macfarlanei* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xii + 30 pp. www.registrelep-sararegistry.gc.ca/default_e.cfm.
- *DAVIS H, WEIR R. 2008. Western Screech-Owl conservation along the Shuswap River: Final report. BCRP Project # 07.W.SHU.01. Armstrong, BC: Artemis Wildlife Consultants. 97p. Available from: BC Hydro Bridge Coastal Restoration Program. http://www.bchydro.com/bcrp/projects/docs/bridge_river/06.W.SHU.02.pdf.
- DAVIS H, WEIR R. 2010. Home ranges and spatial organization of Western Screech-Owls in southern British Columbia. *Northwestern Naturalist* 91:157–164.
- DEMARCHI DA. 1995. Ecoregions of British Columbia. Victoria, BC: Ministry of Environment, Lands and Parks.
- DRUGGER KM, WAGNER F, ANTHONY RG, OLSON GS. 2005. The relationship between habitat characteristics and demographic performance of Northern Spotted Owls in southern Oregon. *Condor* 4:863–878.
- ELLIOT K. 2006. Declining numbers of Western Screech-Owl in the lower mainland of British Columbia. *British Columbia Birds* 14:2–11.
- FLESCH AD, STEIDL RJ. 2010. Importance of environmental and spatial gradients on patterns and consequences of resource selection. *Ecological Applications* 20:1021–1039.
- FORSMAN ED, ANTHONY RG, DUGGER KM, GLENN EM, FRANKLIN AB, WHITE GC, SCHWARZ CJ, BURNHAM KP, ANDERSON DR, NICHOLS JD, HINES JE, LINT JB, DAVIS RJ, ACKERS SH, ANDREWS LS, BISWELL BL, CARLSON PC, DILLER LV, GREMEL SA, HERTER DR, HIGLEY JM, HORN RB, REID JA, ROCKWEIT J, SCHABERL JP, SNETSINGER TJ, SOVERN SG. 2011. Population demography of Northern Spotted Owls. *Studies in Avian Biology*, No. 40. Berkeley and Los Angeles, CA: University of California Press. 105 p.
- HAKKARAINEN H, KORMIMÄKI E, LAAKSONEN T, NIKULA A, SUORSA P. 2007. Survival of male Tengmalm's Owls increases with cover of old forest in their territory. *Oecologia* 155:479–486.
- HERTLING BL, BELTHOFF JR. 1997. Testosterone, aggression and territoriality in male Western Screech-Owls (*Otus kennicottii*): Results from preliminary experiments. In: Duncan JR, Johnson DH, Nicholls TH, editors. *Biology and conservation of the owls of the northern hemisphere*: 2nd in-

* Unpublished

- ternational symposium. St Paul, MN: US Department of Agriculture, Forest Service, North Central Forest Experiment Station, General Technical Report NC-190. p 213–217.
- HERTLING BL, BELTHOFF JR. 2001. Bounce and double trill songs of male and female Western Screech-Owls: Characterization and usefulness for classification of sex. *The Auk* 118:1095–1101.
- KAPLAN EL, MEIER P. 1958. Nonparametric estimation from incomplete observations. *Journal of American Statistical Association* 53:457–481.
- KARELL P, AHOLA K, KARSTINEN T, ZOLEI A, BROMMER JE. 2009. Population dynamics in a cyclic environment: Consequences of cyclic food abundance on Tawny Owl reproduction and survival. *Journal of Animal Ecology* 78:1050–1062.
- LEBRETON JD, BURNHAM KP, CLOBERT J, ANDERSON DR. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs* 62:67–118.
- LIKER A, SZÉKELY T. 2005. Mortality costs of sexual selection and parental care in natural population of birds. *Evolution* 59:890–897.
- MAGDALENA LA, SEETHER BE, ENGEN S. 2011. Demographic stochasticity, allee effects, and extinction: The influence of mating system and sex ratio. *American Naturalist* 3:301–313.
- MILLON A, PETTY SJ, LAMBIN X. 2010. Pulsed resources affect the timing of first breeding and lifetime reproductive success of Tawny Owls. *Journal of Animal Ecology* 79:426–435.
- [MWLAP] MINISTRY OF WATER, LAND AND AIR PROTECTION. 2004. Procedures for managing identified wildlife – V. 2004. Victoria, BC: BC Ministry of Water, Land and Air Protection. <http://www.env.gov.bc.ca/wld/frpa/iwms/procedures.html>.
- POLLOCK KH, WINTERSTEIN SR, BUNCK CM, CURTIS PD. 1989. Survival analysis in telemetry studies: The staggered entry design. *Journal of Wildlife Management* 53:7–15.
- PRESTON MI, POWERS GA. 2006. High incidence of vehicle induced owl mortality in the Lower Mainland and Central Fraser Valley, British Columbia. *Wildlife Afield* 3:15–23.
- SEVERINGHAUS LL, ROTHERY P. 2001. The survival rate of Lanyu Scops Owls *Elegans botelensis*. *Ibis* 143: 540–546.
- SMITH DG, GILBERT R. 1981. Backpack radio transmitter attachment success in screech owls (*Otus asio*). *North American Bird Bander* 6:142–143.
- SMITH JC, SMITH MJ, HILLIARD BL, POWERS LR. 1983. Trapping techniques, handling methods, and equipment use in biotelemetry study of long-eared owls. *North American Bird Bander* 8:46–47.
- SPROAT TM, RITCHISON G. 1993. The nest defence behaviour of Eastern Screech-Owls: Effects of nest stage, sex, nest type and predator location. *The Condor* 95:288–296.
- TRIPP T, OTTER KA. 2006. Vocal individuality as a potential long-term monitoring tool for Western Screech-Owls, *Megascops kennicottii*. *Canadian Journal of Zoology* 84:744–753.
- [WSRT] WESTERN SCREECH-OWL MACFARLANEI SUBSPECIES RECOVERY TEAM. 2008. Recovery strategy for the Western Screech-Owl, *macfarlanei* subspecies (*Megascops kennicottii macfarlanei*) in British Columbia. Prepared for the BC Ministry of Environment, Victoria, BC.
- WHITE GC, BURNHAM KP. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46:120–138.

Submitted 13 August, 2014, accepted 5 March 2015.
Corresponding Editor: D Max Smith.

Copyright of Northwestern Naturalist is the property of Society for Northwestern Vertebrate Biology and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.