

# POST-FLEDGING SURVIVAL OF MARBLED MURRELETS *BRACHYRAMPHUS MARMORATUS* ESTIMATED WITH RADIO-MARKED JUVENILES IN DESOLATION SOUND, BRITISH COLUMBIA

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Received 25 January 2003, accepted 27 June 2003

## SUMMARY

PARKER, N., CAM, E., LANK, D.B. & COOKE, F. 2003. Post-fledging survival of Marbled Murrelets *Brachyramphus marmoratus* estimated with radio-marked juveniles in Desolation Sound, British Columbia. *Marine Ornithology* 31: 207-212.

For many birds, juvenile survival rates are the least-known demographic component. However, such estimates are important in the construction of population projection models. Here we report the first estimates of local survival for juvenile Marbled Murrelets *Brachyramphus marmoratus*, an alcid species of conservation concern in the Pacific Northwest. We estimated the survival of 34 radio-tagged individuals to be 0.8621 (95% CI 0.7250 – 1.001) during an 80 day period post-fledging. When extrapolated over a year, under the assumption of constant survival, this translates into an annual survival rate of 0.51. In the absence of information on the influence of the transmitters on survival, our estimates were calculated with the assumption that there were no effects. Our estimates do not include fledging or early post-fledging mortality. A high proportion of radioed juveniles were censored throughout the study, and we suggest that natal dispersal may account for this. The extrapolated annual survival rate is lower than values previously used in demographic models for this species, but this work provides the first data-based evaluation of juvenile survival for the Marbled Murrelet.

Keywords: Marbled Murrelet, *Brachyramphus marmoratus*, demography, post-fledging survival, dispersal

## INTRODUCTION

Post-fledging juvenile survival rates are difficult to measure, particularly for seabirds (Harris *et al.* 1994, Gaston 1997). However, several studies have highlighted the demographic importance of estimates of survival during the first year, and until first breeding, for both seabirds (e.g. Hudson 1985) and birds in general (e.g. Ganey *et al.* 1998, Hafner *et al.* 1998). Such estimates are particularly important in the construction of population projection models (e.g. Caswell 2001). Commonly used in studies with conservation implications, these models provide a standard analytical tool for estimating population growth rates as well as assessing the possible consequences of changes in various demographic parameters to these rates.

The Marbled Murrelet *Brachyramphus marmoratus* breeds in coastal old-growth forest from California to Alaska. The species is currently listed as threatened or endangered over much of its range, and the fate of these populations is linked to management decisions, which may be more effective and reliable with knowledge of the demography of the population. Despite this urgent need for a careful assessment of Marbled Murrelet population trends (Cooke 1999) estimates of several of the vital rates, including juvenile survival, are rare or missing (Ralph & Long 1995, Beissinger & Nur 1997, Boulanger *et al.* 1999). However, recent work (Cam *et al.* 2003, Bradley *et al.* 2002) has been successful in partially filling these gaps.

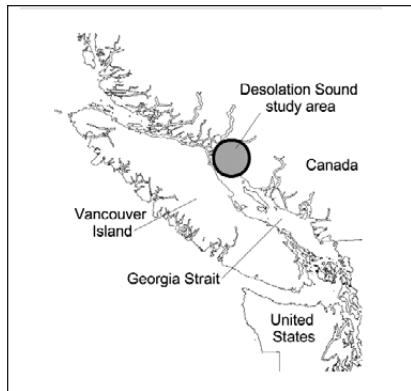
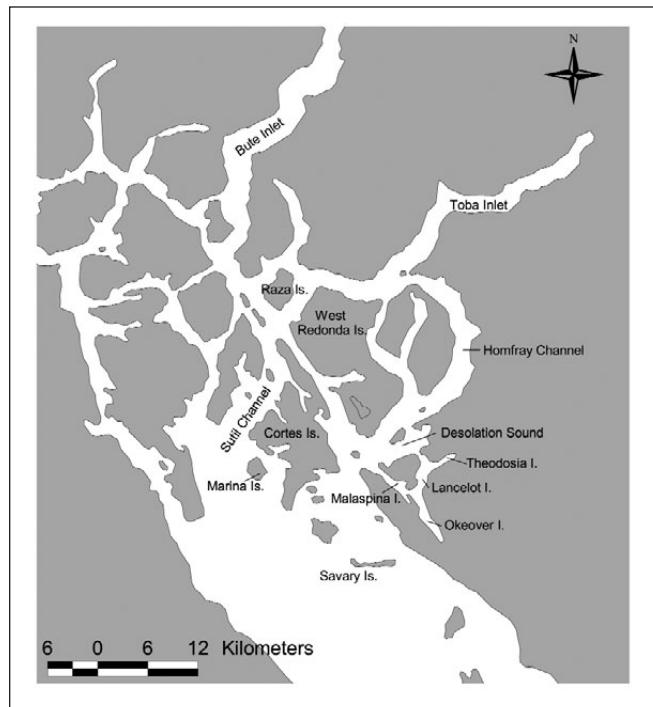
In the absence of studies of individually marked murrelets, estimates of annual juvenile survival for the Marbled Murrelet have previously been estimated by extrapolation from values calculated for other alcid species, and modified on the assumption that smaller alcids have lower survival rates than larger ones (see Beissinger 1995). These values have been used in population projection models to assess population growth rate (Beissinger 1995, 1997). This is the only possible approach in the absence of field data, but it is impossible to assess whether the adjustments chosen are realistic. Under any circumstances, it is best to assess population growth using data from the population(s) about which one wants to draw inferences. Parameter values from other species may differ substantially from those of the study population(s) (Cam *et al.* 2003).

Here, we report the first direct estimates of local survival rates of juvenile Marbled Murrelets, using field data from Desolation Sound, British Columbia, Canada. The Sound is a major feeding and staging area for murrelets and has been the site of a research programme investigating the demography and breeding biology of the species since 1994 (Cooke 1999, Hull *et al.* 2001, Bradley 2002, Lougheed *et al.* 2002, Cam *et al.* 2003, McFarlane-Tranquilla *et al.* 2003). Despite the longer term nature of the banding project at this site, Cam *et al.* (2003) documented that recapture rates of marked adults were extremely low, and that of juveniles marked after fledging too low to provide a meaningful estimate of local survival rate. We therefore directly investigated local juvenile survival with a telemetry study in 2001. A pilot

project in and around the Sound during the 2000 season met with success in tracking radioed juveniles and suggested that post-fledging survival may be high for this area (N. Parker unpublished data). Our primary objective was to determine local survival during the early post-fledging phase of a murrelet's life.

## METHODS

From 1997-2000, juvenile Marbled Murrelets were captured in Desolation Sound (centre 50° 05' N, 124° 45' W, Fig. 1), by dipnetting (Whitworth *et al.* 1997), as part of a larger banding effort for the population as a whole (see Cam *et al.* 2003). The dipnet effort typically began in mid-April of each year, and continued until mid-August (1997, 1998, 2000) or early September (1999). Juveniles were captured from the time of their first appearance on the water, usually from mid- to late June each year. Captured individuals were banded with size 3 stainless steel US Fish and Wildlife Service/Canadian Wildlife Service bands. We tallied recaptures of these birds.



**Fig. 1.** Study area in Desolation Sound, British Columbia.

During the 2001 season, and based on prior knowledge of the breeding chronology of this population (McFarlane-Tranquilla *et al.*, in press), captures began on June 10, 2001 before the first appearance of fledglings on the water. The first juvenile was tagged on June 25 and the last on August 11.

Captured individuals were banded with size 3 stainless steel US Fish and Wildlife Service/Canadian Wildlife Service bands as for previous years. In addition, radio transmitters (3.2g Model 386, depth ~4mm, diameter 3.5mm, Advanced Telemetry Systems, Inc., Isanti, Minnesota) were attached to 34 individuals following the methods of Newman *et al.* (1999) but without sutures or anaesthetic. In addition to the subcutaneous anchor, the end of the transmitter was secured to the feathers with a small amount of 3M Vettbond™ Tissue Adhesive. Body coverts were then 'preened' over the unit.

Birds were tracked daily from a 5.2 m Boston Whaler, weather permitting. The study area as defined for tracking, based on the pilot project in 2000, incorporated adjacent Malaspina, Lancelot and Theodosia Inlets, and extended south to Savary Island, north to Bute Inlet, east to Homfray Channel, and west to Marina Island and the Sutil Channel (Fig. 1). The frequencies of the 34 individuals in the study were scanned from waypoints within the study area.

Although tracking began immediately following the initial captures, survival rate was estimated over eight time intervals of 10 days each, beginning July 9, 2001 and ending 26 September, 2001. We define post-fledging survival rate for the period as that estimated between these dates. The start date of 9 July 2001 corresponded to the time taken to capture a sufficient sample (n=15) to allow estimation of survival (Pollock *et al.* 1989, see also Bennetts *et al.* 1999). Tracking continued until late September. Each transmitter (Model 386) has an insured life of 80 days, and although the theoretical life expectancy (and actual, Centre for Wildlife Ecology Marbled Murrelet Project unpubl. data) is often double this, the tracking period corresponded to the insured life expectancy of the first transmitters deployed (Kenward 2001).

During each 10-day survival interval, marked individuals were located visually at least once to verify their fate. Fixed-wing tracking was initiated once we were unable to efficiently locate all juveniles from the water, within each time interval. Crews attempted to locate each individual by boat as soon as possible following flights. Extended flights were also conducted periodically in an attempt to locate censored individuals (see below) that had potentially moved beyond the range of the defined study area.

## Survival estimation

We estimated the post-fledging survival rate of radio-tagged juveniles within our study area using a modification of the Kaplan-Meier method developed by Pollock *et al.* (1989). This method allows for staggered entry (i.e., not all animals are radio-tagged at the same time), and for the use of right-censored data resulting from radio failure or inability to relocate an individual once tagged (White & Garrott 1990). To avoid biasing our estimates high, we permanently censored all cases when we failed to detect a signal in a given time interval, regardless of whether the individual was subsequently detected inside the study area (see Bunck & Pollock 1993 and Bunck *et al.* 1995). We also censored individuals whose signal was detected outside the defined study area (Bunck &

Pollock 1993). Due to small sample sizes, we did not consider models allowing survival to vary with date of entry, or mass at capture (e.g. Harris & Rothery 1984, Harris *et al.* 1992, Gaston 1997).

## RESULTS

Between 1997 and 2000 inclusive, a total of 106 juveniles have been banded within Desolation Sound. Of these, only two have been subsequently recaptured, both in the year following initial capture. No individuals banded as juveniles within the Sound have been detected breeding within the study area.

We estimated the survival of the 34 radiotagged juveniles during the 80 day period post-fledging to be 0.8621 (95% CI 0.7250 – 1.001, Table 2). Three juveniles were confirmed dead (Table 1). Two of these radios were tracked to trees containing eagle nests, and the third was found in an area with eagle sign. Although we cannot rule out the possibility that the carcasses were scavenged following death from other causes, Bald Eagle (*Haliaeetus leucocephalus*) predation thus seems the likely cause. Nineteen individuals were censored, of which 12 were not detected again following censoring, five were subsequently resighted at least once inside the study area, and two (Frequencies 4.111 and 5.843) were subsequently detected outside the study area. Frequency 4.111 (captured before interval 1, censored in interval 2) was detected north of Desolation Sound, on the mainland coast at the entrance to Queen Charlotte Strait (Fig. 2). In contrast Frequency 5.843

(captured in interval 2, censored in interval 4) was detected to the south, along the east coast of Vancouver Island, on three separate occasions (Fig. 2).

## DISCUSSION

Our estimate of immediate post-fledging survival is based on the first such data for both the Marbled Murrelet specifically, and for alcids in general. There was no evidence of high mortality immediately following marking, consistent with observations made during the pilot project in 2000, and also as noted by Lougheed *et al.* (2002).

We estimated a survival rate of 0.8621 for the first 80 days following capture (post-fledging survival). Based on an assumption that survival is constant over time, we extrapolated an annual survival of 0.51. The only other values for Marbled Murrelets are those of Beissinger (1995), where first year survival was assumed to be 70% that of adult survival, as suggested by Nur (1993). Using a range of survival rates for adults, Beissinger (1995) calculated a corresponding range for first year survival from 0.595–0.63. Our estimate falls below this range, but not substantially so. With regard to other alcids, most estimates of juvenile survival are reported as survival to first breeding as determined from resighting and banding recoveries in natal colonies (summaries in Hudson 1985 and Gaston and Jones 1998), which means that the survival estimate covers two or three years, and also assumes natal philopatry. However, Ydenberg (1989) presented estimates of first-year mortality using the same data from Hudson (1985). If we consider these in terms of first-year survival (i.e. 1-mortality), and use only those calculated on the assumption that mortality is highest in the first year ('method B', Ydenberg 1989), values for the atlantic alcids ranged from 0.29–0.46. In comparison, our value is higher, but not substantially so.

The following should be considered if applying our estimates more broadly. Firstly, both the 80 day and the annual extrapolations are based on data from birds carrying radio transmitters. However, Cam (unpubl. data) could not detect an influence of radios on the survival or recapture probability of adults in the Desolation Sound population, thus we have no reason to expect a large influence on juveniles. We therefore made the assumption that the transmitters did not affect individual survival.

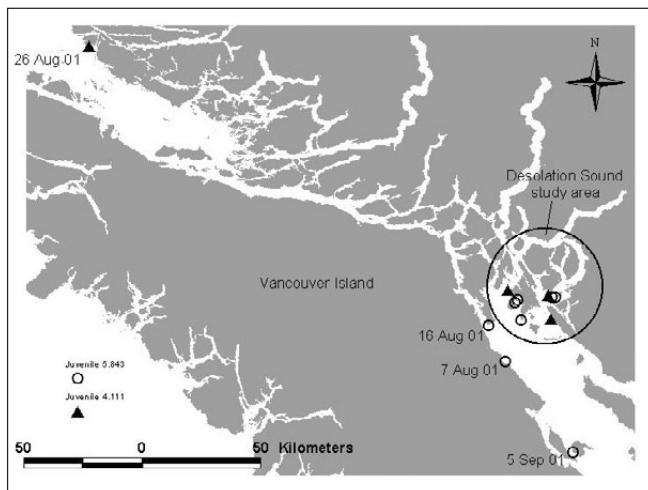


Fig. 2. Movements of two censored individuals, outside the defined study area.

TABLE 1  
Data from Radio-tagged juvenile Marbled Murrelets  
in British Columbia, Canada

Occasion	Number at risk	Number dead	Number censored	Number added
1	15	0	0	15
2	30	1	3	2
3	28	1	3	0
4	24	0	10	2
5	16	0	0	0
6	16	1	1	0
7	14	0	1	0
8	13	0	1	0

TABLE 2  
Kaplan-Meier estimates of local survival in juvenile  
Marbled Murrelets for each time interval (July–September).

Occasion	Kaplan-Meier survival estimate	95% Confidence Interval
1	1.0000	1.0000 – 1.0000
2	0.9623	0.8990 – 1.0269
3	0.9244	0.8343 – 1.0145
4	0.9244	0.8343 – 1.0145
5	0.9244	0.8343 – 1.0145
6	0.8628	0.7250 – 1.001
7	0.8621	0.7250 – 1.001
8	0.8621	0.7250 – 1.001

Secondly, we estimated survival over a period of 80 days post-fledging, and extrapolated this, assuming constant mortality, to estimate annual survival. However, our assumption is probably unrealistic, and the resulting annual local survival estimate should be used judiciously. Juvenile survival rates for avian species may not be constant from fledging and throughout the first year. Instead periods of increased vulnerability and high mortality in that first year are commonly documented (Hudson 1985) and are usually seen as a consequence of increased risk in association with fledging and independence (Harris *et al.* 1992, Rohner & Hunter 1996), dispersal (Beaudette & Keppie 1992, Bennetts & Kitchens 1999), or the changing environmental conditions encountered during the first winter (Harris *et al.* 1994, Kersten and Brenninkmeijer 1995).

Our estimates do not account for fledging or extremely early post-fledging mortality. We used data from juveniles that successfully flew from the nest to the water and survived during a period of time of unknown length (from fledging to capture). The long flight from the nest to the ocean can be hazardous, as indicated by findings of grounded young (Carter & Sealy 1987, Rodway *et al.* 1992). The first days that follow fledging could be crucial to the survival of juvenile Marbled Murrelets as they begin to forage on their own and disperse into unfamiliar areas. Radio-equipped juveniles in this study were most frequently seen alone and in areas with fewer murrelets in general, indicating little or no post-fledging parental care (N. Parker unpubl. data, see also Kuletz & Marks 1997). This is consistent with observations for other semi-preocial Atlantic alcids (Atlantic Puffin, Black Guillemot and Dovekie, Harris & Rothery 1984, Harris & Birkhead 1985), but contrasts with a statement in Ydenberg (1989) for Marbled Murrelets. Although we attempted to catch birds as young as possible, it is likely that some birds in our sample had already survived several days on the water before capture.

Thirdly, juvenile survival has been shown to vary significantly on an annual basis for a number of seabirds (eg Harris *et al.* 1992, Harris *et al.* 1994), and for birds in general (eg Hafner *et al.* 1998, Bennetts *et al.* 1999). This parameter can also vary among regions for the same species in the same year (eg Bennetts *et al.* 1999). Further studies are needed to address the spatial and temporal variation in juvenile survival for Marbled Murrelets.

Finally, radio-telemetry studies can underestimate true survival (i.e. the quantity assessed is *local* survival), due to emigration and dispersal from a study area (Hudson 1985, Beissinger 1995), or potentially overestimate survival due to the censoring of individuals that are actually dead (e.g. Bennetts *et al.* 1999). We estimated local survival at a time when it is highly likely that juveniles were dispersing, and this may account for the large number of individuals censored. Indeed seven of the 19 censored individuals were subsequently recontacted, two of these outside the study area. Although, due to our strict criteria we censored these individuals when they were clearly alive, which could lead to the conclusion that we were in fact underestimating survival, 12 of the marked birds remained unaccounted for following censoring. Our local survival estimates are therefore based on data from individuals that remained in the study area during the tracking period.

Natal dispersal (as defined by Greenwood 1980) is common for alcids in general (Harris 1983, Hudson 1985), and may have resulted in the underestimation of juvenile survival in other radio-telemetry and capture mark-recapture studies (Hudson 1985). While very little is known of the post-breeding movements of juvenile Marbled Murrelets (Kuletz & Kendall 1998, Kuletz & Piatt 1999), we can expect dispersal to be high: the winter distribution is extensive, individuals are capable of dispersing great distances, and potential breeding habitat is extensive (Divoky & Horton 1995). The methodologies presented here did not allow a detailed investigation of natal dispersal during this study. However, the opportunistic detections of two censored individuals outside the study area do provide evidence of such dispersal.

A systematic investigation of the dispersal of Marbled Murrelets from Clayoquot Sound in 2002 documented the movement of radioed juveniles northward along the coast of Vancouver Island, and onto the mainland coast, after leaving the Sound. While this movement was initiated within days of capture for some individuals, others remained within the Sound, or near vicinity, for up to 60 days before dispersing north (Parker *et al.* MS). It is therefore not unreasonable to expect that natal dispersal confounded the estimates we present, and indeed may also account for the extremely low numbers of banded juveniles recaptured in the study area.

In studies investigating juvenile survival rates from mark-recapture and radio telemetry methods simultaneously, mark-recapture (Bennetts *et al.* 1999) or a combination of the two has been found to be preferable (Powell *et al.* 2000). As reported here the number of marked juveniles recaptured in our study area is very low. We might have expected by this time that these individuals would begin returning earlier, in greater numbers and for longer periods as they approach breeding age (e.g. Lloyd & Perrins 1977, Harris 1983, see also Gaston and Jones 1998). Despite the longer term nature of the project, we currently have little data to confidently document the age of first breeding for this species from individuals banded as juveniles. With current methodologies, and limited knowledge of natal dispersal, it may prove impossible to determine survival until first breeding in the Marbled Murrelet. Despite the limitations of our results, their value should therefore be considered in the context of current knowledge for Marbled Murrelets specifically and for seabirds in general.

## ACKNOWLEDGEMENTS

We would like to thank the field crew of 2001 for their tireless efforts in keeping track of the birds they also radioed. Parallel Aviation in Campbell River provided the fixed-wing support. Financial support was provided by Forest Innovation Investment, Forest Renewal BC, both through the Science Council of BC and through the Multi-Year Agreement; the Natural Sciences and Engineering Research Council of Canada; the National Council of the Paper Industry for Air and Stream Improvement, Inc.; Weyerhaeuser Canada Ltd.; International Forest Products Ltd.; the Canadian Wildlife Service and the Centre for Wildlife Ecology at Simon Fraser University.

## REFERENCES

BEAUDETTE, P.D. & KEPPIE, D.M. 1992. Survival of dispersing spruce grouse. *Canadian Journal of Zoology*. 70: 693-697.

BEISSINGER, S.R. 1995. Population trends of the Marbled Murrelet projected from demographic analyses. In: Ecology and Conservation of the Marbled Murrelet. Ralph, C.J., Hunt Jr., G.L., Raphael, M.G. & Piatt, J.F. (Eds.). USDA Forest Service General Technical Report PSW-GTR-152. pp. 385-393.

BEISSINGER, S.R. & NUR, N. 1997. Population trends of the Marbled Murrelet projected from demographic analysis. In: Recovery Plan for the Threatened Marbled Murrelet (*Brachyramphus marmoratus*) in Washington, Oregon, and California. Portland, Oregon. U. S. Fish and Wildlife Service.

BENNETTS, R.E., DREITZ, V.J., KITCHENS, W.M., HINES, J.E. & NICHOLS, J.D. 1999. Annual survival of snail kites in Florida: radio telemetry versus capture-resighting data. *Auk* 116(2): 435-447.

BENNETTS, R.E. & KITCHENS, W.M. 1999. Within year survival patterns of snail kites in Florida. *Journal of Field Ornithology* 70: 268-275.

BOULANGER, J., MARTIN, K.M., KAISER, G.W. & BOYD, W.S. 1999. Evaluating uncertainty in estimating population trends of Marbled Murrelets. In: Biology and Conservation of Forest Birds. Diamond, A.W. & Nettleship, D.N. (Eds.). Society of Canadian Ornithologists Special Publication No. 1. Fredericton, New Brunswick. pp. 53-63.

BRADLEY, R.W. 2002. Breeding ecology of radio-marked Marbled Murrelets (*Brachyramphus marmoratus*) in Desolation Sound, British Columbia. Unpub. Masters Thesis. Simon Fraser University, Burnaby, BC.

BUNCK, C.M. & POLLOCK, K. H. 1993. Estimating survival of radio-tagged birds. In: Marked Individuals in the Study of Bird Population. Lebreton, J.D. & North, P. M. (Eds.). Birkhäuser Verlag Basel/Switzerland. pp. 51-63.

BUNCK, C.M., CHEN, C. & POLLOCK, K.H. 1995. Robustness of survival estimates from radio-telemetry studies with uncertain relocation of individuals. *Journal of Wildlife Management* 59:790-794.

CAM, E., LOUGHEED, L., BRADLEY, R. & COOKE, F. 2003. Demographic assessment of a Marbled Murrelet population from capture-recapture data. *Conservation Biology* 17: 1-10.

CARTER, H.R. & SEALY, S.G. 1987. Inland records of downy young and fledgling Marbled Murrelets in North America. *Murrelet* 68: 58-63.

CASWELL, H. 2001. Matrix population models: Construction, analysis, and interpretation, 2nd Ed. Sinauer Associates, Inc., Sunderland, Massachusetts.

COOKE, F. 1999. Population studies of Marbled Murrelets (*Brachyramphus marmoratus*) in British Columbia. In: Biology and Conservation of Forest Birds. Diamond, A.W. & Nettleship, D.N. (Eds.). Society of Canadian Ornithologists Special Publication No. 1. Fredericton, New Brunswick. pp. 43-51.

DIVOKY, G.J. & HORTON, M. 1995. Breeding and natal dispersal, Nest Habitat Loss and Implications for Marbled Murrelet Populations. In: Ecology and Conservation of the Marbled Murrelet. Ralph, C.J., Hunt Jr., G.L., Raphael, M.G. & Piatt, J.F. (Eds.). USDA Forest Service General Technical Report PSW-GTR-152. pp. 83-88.

GANEY, J.L., BLOCK, W.M., DWYER, J. K., STROHMEYER, B.E. & JENNESS, J.S. 1998. Dispersal movements and survival rates of juvenile mexican spotted owls in Northern Arizona. *Wilson Bulletin* 110: 206-217.

GASTON, A.J. 1997. Mass and date at departure affect the survival of Ancient Murrelet *Synthliboramphus antiquus* chicks after leaving the colony. *Ibis* 139: 673-678.

GASTON, A.J. & I.L. JONES. 1998. The Auks. Oxford University Press, Oxford. pp. 349.

GREENWOOD, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28: 1140-1162.

HAFNER, H., KAYSER, Y., BOY, V., FASOLA, M., JULLIARD, A., PRADEL, R. & CÉZILLY, F. 1998. Local survival, natal dispersal, and recruitment in Little Egrets *Egretta garzetta*. *Journal of Avian Biology* 29: 216-227.

HARRIS, M.P. 1983. Biology and survival of the immature Puffin *Fratercula arctica*. *Ibis* 125: 56-73.

HARRIS, M.P. & ROTHERY, P. 1984. The post-fledging survival of young Puffins *Fratercula arctica* in relation to hatching date and growth. *Ibis* 127: 243-250.

HARRIS, M.P. & BIRKHEAD, T.R. 1985. Breeding ecology of the Atlantic Alcidae. In: The Atlantic Alcidae. The evolution, distribution and biology of the Auks inhabiting the Atlantic Ocean and adjacent water area. Nettleship, D.N. & Birkhead, T.R. (Eds.). Academic Press, NY. pp. 155-204.

HARRIS, M.P., HALLEY, D. J. & WANLESS, S. 1992. The post-fledging survival of young Guillemots *Uria aalge* in relation to hatching date and growth. *Ibis* 134: 335-339.

HARRIS, M.P., BUCKLAND, S.T., RUSSELL, S.M. & WANLESS, S. 1994. Post fledging survival to breeding age of Shags *Phalacrocorax aristotelis* in relation to year, date of fledging and brood size. *Journal of Avian Biology* 25: 268-274.

HUDSON, P.J. 1985. Population parameters for the atlantic alcidae. In: The Atlantic Alcidae. The evolution, distribution and biology of the Auks inhabiting the Atlantic ocean and adjacent water area. Nettleship, D.N. & Birkhead, T.R. (Eds.). Academic Press, NY. pp. 233-261.

HULL, C.L., KAISER, G.W., LOUGHEED, C., LOUGHEED, L., BOYD, S., & COOKE, F. 2001. Intra-specific variation in commuting distance of Marbled Murrelets (*Brachyramphus marmoratus*): ecological and energetic consequences of nesting further inland. *Auk* 118: 1036-1046.

KENWARD, R.E. 2001. A manual for wildlife radio tagging. Academic Press, NY.

KERSTEN, M. & BRENNINKMEIJER, A. 1995. Growth, fledging success and post-fledging survival of juvenile Oystercatchers *Haematopus ostralegus*. *Ibis* 137:396-404.

KULETZ, K.J. & MARKS, D. K. 1997. Post-fledging behavior of a radio-tagged juvenile Marbled Murrelet. *Journal of Field Ornithology* 68: 424-425.

KULETZ, K.J. & KENDALL, S. J. 1998. A productivity index for Marbled Murrelets in Alaska based on surveys at sea. *Journal of Wildlife Management* 62: 446-460.

KULETZ, K.J. & PIATT, J. F. 1999. Juvenile Marbled Murrelet nurseries and the productivity index. *Wilson Bulletin* 111: 257-261.

LLOYD, C.S. & PERRINS, C. M. 1977. Survival and age at first breeding in the razorbill (*Alca torda*). *Bird Banding* 48: 239-252.

LOUGHEED, C., LOUGHEED, L., COOKE, F. & BOYD, S. 2002. Local survival of adult and juvenile Marbled Murrelets and their importance for estimating reproductive success. *Condor* 104: 309-318.

MCFARLANE-TRANQUILLA, L., WILLIAMS, T. & COOKE, F. 2003. The reliability of brood patches in assessing reproductive status in the Marbled Murrelet: Words of caution. *Waterbirds* 26:108-118.

MCFARLANE-TRANQUILLA, L., WILLIAMS, T. & COOKE, F. In press. Using physiology to examine interannual variation in breeding chronology of Marbled Murrelets in Desolation Sound, B.C. *Auk*.

NEWMAN, S.H., TAKEKAWA, J.Y., WHITWORTH, D.L. & BURKETT, E. E. 1999. Subcutaneous anchor attachment increases retention of radio transmitters on Xantus' and Marbled Murrelets. *Journal of Field Ornithology* 70: 520-534.

NUR, N. 1993. Establishing the demographic parameters of the Marbled Murrelet. Report on file. Portland, OR: U. S. Fish and Wildlife Service.

POLLOCK, K.H., WINTERSTEIN, S.R., BUNCK, C.M. & CURTIS, P.D. 1989. Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* 53: 7-15.

POWELL, L.A., CONROY, M.J., HINES, J.E., NICHOLLS, J.D. & KREMENTZ, D.G. 2000. Simultaneous use of mark-recapture and radiotelemetry to estimate survival, movement, and capture rates. *Journal of Wildlife Management* 64: 302-313.

RALPH, C.J. & LONG, L.L. 1995. Productivity of Marbled Murrelets in California from observations of young at sea. In: *Ecology and conservation of the Marbled Murrelet*. Ralph, C.J., Hunt, Jr. G.L., Raphael, M.G. & Piatt, J.F. (Eds.). General Technical Report PSW-GTR-152. Albany, CA: Pacific Southwest Research Station, Forest Service, US Dept. of Agriculture. pp. 371-377

RODWAY, M.S., CARTER, H.R., SEALY, S.G. & CAMPBELL, R.W. 1992. Status of the Marbled Murrelet in British Columbia. *Proceedings of the Western Foundation of Vertebrate Zoology* 5: 17-41.

ROHNER, C. & HUNTER, D.B. 1996. First-year survival of great horned owls during a peak and decline of the snowshoe hare cycle. *Canadian Journal of Zoology* 74: 1092-1097.

WHITE, G.C. & GARROTT, R.A. 1990. Analysis of wildlife radio-tracking data. Academic Press, NY.

WHITWORTH, D.L., TAKEKAWA, J.Y., CARTER, H.R. & MCIVER, W.R. 1997. A night lighting technique for at sea capture of Xantus's Murrelets. *Colonial Waterbirds* 20: 525-531.

YDENBERG, R.C. 1989. Growth-mortality trade-offs and the evolution of juvenile life histories in the Alcidae. *Ecology* 70(5): 1494-1506.