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The Condor 101:398–402
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EVIDENCE OF MALE-BIAS IN CAPTURE SAMPLES OF MARBLED MURRELETS FROM GENETIC STUDIES IN BRITISH COLUMBIA¹

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Abstract. We report a significant male-bias (1.8:1) in Marbled Murrelets (*Brachyramphus marmoratus*) captured with floating mist nets during the breeding season over four years (1994–1997) at Theodosia Inlet, Desolation Sound, British Columbia. There was little evidence for marked annual or diurnal variation in male-bias, or for variation due to flight direction of birds when they contacted the net (inland vs. out to sea). In contrast, samples of adult and juvenile Marbled Murrelets captured using a night-lighting technique at Desolation Sound in 1997 were not male-biased. We believe that the most likely explanation for our results is that there are sex-specific differences in behavior of Marbled Murrelets during the breeding period, such that more males than females are flying between marine foraging and inland nesting areas.

Key words: *Brachyramphus marmoratus*, male-bias, Marbled Murrelet.

Marbled Murrelets (*Brachyramphus marmoratus*) are atypical among Alcidae and other seabirds in that they

nest predominantly in large trees found in old-growth coniferous forests (Nelson 1997). In recent years, population declines have been observed for Marbled Murrelets over much of their range (Nelson 1997) including parts of British Columbia where the Marbled Murrelet is classified as a "threatened" species (Rodway 1990). Current demographic information is limited to adult:juvenile ratios derived from marine and aerial surveys (Nelson 1997), but interpretation of survey data are difficult if one lacks basic information on population or subpopulation sex ratio and age structure.

In this paper, we report the sex of Marbled Murrelets captured during the breeding season using floating mist-nets and a night-lighting technique. We used a recently developed molecular technique (Griffiths et al. 1996) to sex birds because Marbled Murrelets are sexually monomorphic. This is the largest known-sex sample of Marbled Murrelets ever examined, and these data may have important implications for the conservation and management of this species.

METHODS

FIELDWORK AND CAPTURE OF BIRDS

A floating mist-net system (Kaiser et al. 1995) was used to capture Marbled Murrelets from late May to

¹ Received 15 April 1998. Accepted 17 November 1998.

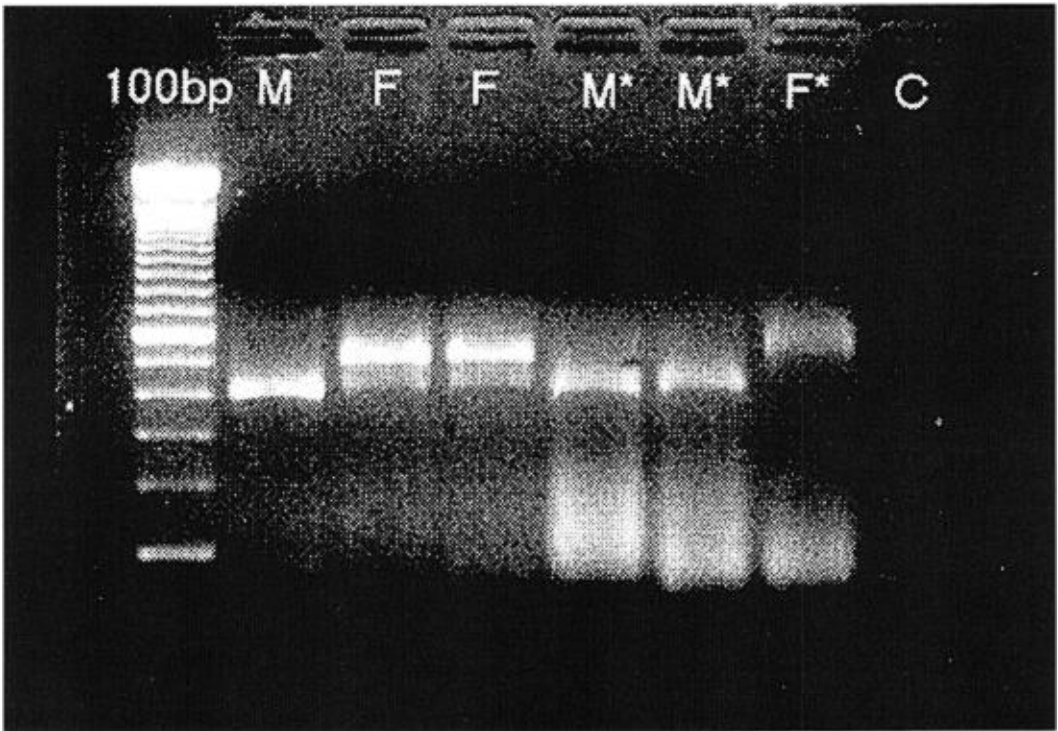


FIGURE 1. Agarose gel showing molecular sex-determining method for Marbled Murrelets. Far left lane contains 100 base pair DNA standard. Males (M) show a single band of approximately 400 base pairs in length, whereas females (F) show two bands of approximately 400 and 470 base pairs in length, respectively. Asterisks denote samples that were sexed successfully from single feathers; all others were from blood samples. The far right lane (C) is a PCR negative control.

mid August over four years (1994–1997; $n = 428$, excluding recaptures) at Theodosia Inlet, Desolation Sound, British Columbia (50°05'N, 124°40'W). An alternative capture technique for Marbled Murrelets, “night-lighting” (Whitworth et al. 1997), was employed concurrently during the 1997 season ($n = 147$). Birds were captured at night (23:00–05:00) on the open waters of Desolation Sound by tracking them with powerful search lights, approaching them stealthily in an inflatable boat powered by an outboard engine, and scooping them into the boat with a salmon landing net. This capture technique also allowed us to capture a small sample of juvenile Marbled Murrelets ($n = 28$) for the first time.

Blood samples (0.5–2.0 ml) were taken from the brachial vein as soon as possible after capture and centrifuged at 5,000 rpm for 10 min. The separated plasma and red blood cell samples were stored at -20°C until further analysis.

DNA EXTRACTION AND MOLECULAR SEXING

Genomic DNA was isolated from erythrocytes in 1994 and 1995 using standard molecular biology techniques (Griffiths et al. 1996), and from samples collected in 1996 and 1997 using Instagene Matrix[™] (Bio-Rad Laboratories, Hercules, California, Cat. No. 732-

6030). Extracted DNA was subjected to PCR amplification following a modification of the methods described by Griffiths et al. (1996), using the two primers P2 (5'-TCTGCATCGCTAAATCCTTT) and CW (5'-AGAAATCATTCCAGAAGTTCA). The resulting PCR products (~470 base pairs) were digested with the restriction enzyme *HaeIII*, and then separated by electrophoresis in a 2% agarose gel and visualized under ultra-violet light. Male birds were identified by the presence of a single 400-bp band and females by the presence of both 470 and 400-bp bands (Fig. 1). The technique also was attempted on feather samples (underwing coverts) from birds already sexed from blood (Fig. 1), but success was rare. Full details of the technique and modifications are available from the senior author.

DATA ANALYSIS

Male-bias in Marbled Murrelet samples and variation in male-bias due to time of capture or flight direction were analyzed for all years with chi-square tests. To examine changes in male-bias within and between years, each season was divided into 15-day intervals beginning on June 1, and a generalized linear model was used to test for variation in male-bias, and chi-square tests were performed to test for linear trends in

TABLE 1. Sex ratio of Marbled Murrelets (excluding intra-year recaptures) captured by mist-netting and night-lighting, and chi-square tests performed with the expectation of a 1:1 sex ratio. Asterisk denotes the exclusion of inter-year recaptures.

Year	No. males	No. females	Sex ratio (M:F)	χ^2_1	P
1994	48	19	2.5	12.6	<0.001
1995	80	42	1.9	11.8	<0.001
1996	66	38	1.7	7.5	<0.01
1997	121	69	1.8	14.2	<0.001
Total (mist-net)*	275	153	1.8	34.8	<0.001
1997 dip net adults	61	58	1.1	0.1	>0.7
1997 dip net juveniles	15	13	1.2	0.1	>0.7

male-bias (Mantel-Haenszel Chi-square test for linear trends, SAS Institute 1996). Due to small sample sizes (<10–15 birds), it was difficult to examine seasonal patterns of male-bias within each year. In 1994, only males were captured in the first 15-day period (June 1–15), and sample sizes after July 1 were relatively small compared to other years, so the data from 1994 were excluded from our analyses. The last 15-day period in each year of the remaining years suffered from small sample sizes, so it was excluded from our analyses.

RESULTS

VALIDATION OF SEXING TECHNIQUE

We sexed 18 Marbled Murrelet carcasses using the molecular sexing technique and then by dissection and gonadal examination. In all cases (18/18), the sex determined using the molecular technique was the same as that determined by dissection. In addition, for >60 mist-netted birds, two or more blood samples were obtained through inter and intra-year recaptures, and in all but three cases (~95%) the sex was classified as being the same for both samples. We believe that these three cases resulted from incorrect sample labeling in the field, rather than a flaw in a molecular sexing technique that has been validated in many avian species (Griffiths et al. 1996).

MALE-BIAS OF MIST-NETTED AND NIGHT-LIGHTED BIRDS

The sample of birds captured in floating mist-nets was significantly male-biased in all four years (Table 1). The male-bias did not differ significantly among years ($\chi^2_3 = 1.56$, $P > 0.60$), and the overall male-bias, pooling all four years, was 1.8 males to 1 female (Table 1). Pooling all years, there was a significant male-bias (24:7) among birds holding fish (presumed chick-feeding birds) when they contacted the floating mist-nets ($\chi^2_1 = 9.2$, $P < 0.01$). Pooling all years, there was a significant male-bias among within-year recaptures ($\chi^2_1 = 10.9$, $P < 0.01$) and between-year recaptures ($\chi^2_1 = 20.9$, $P < 0.001$). There was no significant male-bias in our samples of night-lighted adult and juvenile Marbled Murrelets (Table 1).

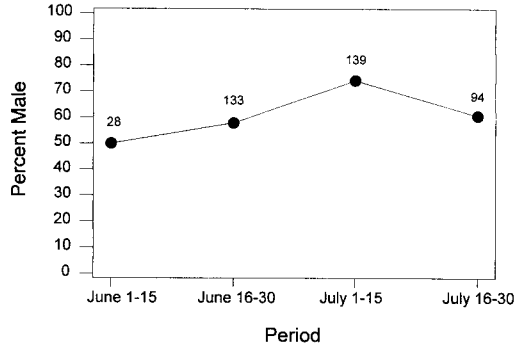


FIGURE 2. Proportion of male Marbled Murrelets captured in floating mist-nets pooled from 1995–1997 by 15-day intervals. Numbers above points are sample sizes.

We examined a number of possible sources of variation that might provide an explanation for this unexpected bias in the sample of birds captured with floating mist-nets. Pooling data for 1995–1997, there was a marginally significant effect of 15-day period ($\chi^2_3 = 7.81$, $P = 0.05$, Fig. 2), but no significant linear trend in male-bias with time ($\chi^2_1 = 1.04$, $P > 0.30$). However, when we restricted our analysis to the early part of the season (June 1–July 15), the male-bias increased significantly with time ($\chi^2_1 = 8.87$, $P < 0.01$, Fig. 2).

Pooling data for all four years, there was no significant difference in male-bias among morning (04:00–07:00) and evening (21:00–00:00) captures ($\chi^2_1 = 0.22$, $P > 0.60$), or in relation to the direction birds were flying when they contacted the floating mist-nets ($\chi^2_1 = 1.32$, $P > 0.2$). In other words, all captures were strongly male-biased.

DISCUSSION

The markedly male-biased sample we observed for Marbled Murrelets captured using floating mist-nets, might be explained in three ways. First, the male-bias reflected a true male-bias at the population level (Breitwisch 1989). Second, the male-bias was a local effect, dependent entirely on sex-specific differences in behavior within Theodosia Inlet. Third, the male-bias was due to capture technique, where males are more easily captured than females.

Our samples of adult and juvenile Marbled Murrelets captured by night-lighting were not significantly male-biased, and did not support a population-level explanation for the observed male-bias in Marbled Murrelets captured with floating mist-nets. Historically, there are few sex ratio data available for other populations or samples of Marbled Murrelets, but most samples of Marbled Murrelets have not been reported as significantly male-biased (Sealy 1972, 1975b, Carter and Sealy 1984).

If male Marbled Murrelets carried out a disproportionate amount of chick provisioning (Fasola and Saino 1995), then the probability of capturing a male would be greater than that for a female due to more frequent flights between the sea and inland nesting

sites. Two of our observations support this hypothesis. First, there was an increase in male-bias from mid-June to the end of July, which is coincident with the transition from incubation to chick-rearing (Hamer and Nelson 1995). Second, we found a significant male-bias in birds holding fish (presumed chick-feeding birds; Carter and Sealy 1987) when they were captured. However, Marbled Murrelets appear to display biparental care, with incubation shared equally between the sexes and both parents participate in feeding the chick (Nelson 1997). As detailed observations on greater numbers of nests become available, it may be possible to test if one parent provisions the chick with greater frequency than the other.

The observed male-bias may have been the result of a surplus of nonbreeding males or failed breeders. Only five birds in our sample captured in floating mist-nets lacked a brood patch (3 males, 2 females), and among our night-lighted sample of adults, only 11 adults (5 males, 6 females) lacked a brood patch, making it unlikely that significant numbers of nonbreeders were in either sample. Very few failed Marbled Murrelet nests have been observed to be re-used in the same season (Nelson 1997), but a bimodal peak in nesting chronology in California suggests that re-nesting after failure or double brooding may be possible (Hamer and Nelson 1995). Thus, the male-bias could be a result of failed male breeders remaining close to nesting habitats, possibly to obtain or retain nesting sites.

Alternatively, equal numbers of birds of each sex may have been available for capture, but our capture methods were somehow nonrandomly sampling males (Domènech and Senar 1998). If males and females take different flight routes to and from the nest, for example due to differences in predation risk, this could affect their probability of capture. However, studies have shown little differences in morphology between male and female Marbled Murrelets that might predispose one sex to have lower maneuverability or greater wing loading (Sealy 1975a, Pitocchelli et al. 1995). In fact, gravid females would be predicted to have a higher capture probability due to increased wing loading and decreased flight ability (Lee et al. 1996).

We believe that there are sex-specific differences in the behavior of Marbled Murrelets during the breeding period. Evidently, more males than females are flying low (just above the water surface, 1–2 m) between marine foraging and inland nesting areas, thus more males are available for capture. In the absence of data supporting or refuting any particular explanation for the observed male-biased sample, the cause of this bias remains speculative. However, our results have important implications for further research aimed at the conservation and management of Marbled Murrelets. First, unless sex is determined directly, researchers should not immediately assume that any sample of Marbled Murrelets represents a random sample of the population. Second, if local variation in sex ratio exists in Marbled Murrelets, this might have a significant effect on current methods used to estimate breeding productivity and breeding population size which assume a 1:1 sex ratio. This study demonstrates a clear need for a better understanding of possible sex-specific be-

havior patterns to better ensure sound conservation and management decisions for the Marbled Murrelet.

We thank the many people who assisted with fieldwork for this project. Particular thanks are due to Scott Edwards, Curator of the Tissue Collection at the University of Washington Burke Museum, and Alan Burger, University of Victoria, for providing murrelet tissue samples; Gary Kaiser, Canadian Wildlife Service, Andy Derocher, British Columbia Ministry of Forests, and Lynn Lougheed, Doug Bertram and Fred Cooke, CWS/NSERC Wildlife Ecology Research Chair, Simon Fraser University. Permits for capturing and blood sampling Marbled Murrelets were issued by the Canadian Wildlife Service (CWS Banding Permit 10201) and Environment Canada (Environment Canada Scientific Permit: BCSCI971012). This project was supported by grants from Forest Renewal British Columbia (B.C.) through Science Council B.C., Ministry of Forests, B.C., Natural Sciences and Engineering Research Council of Canada, Canadian Wildlife Service, MacMillan-Blodel Ltd., TimberWest Forest Ltd., International Forest Products Ltd., Western Forest Products, Ltd., and Pacific Forest Products Ltd.

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The Condor 101:402–407
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FACILITATION OF SAP-FEEDING BIRDS BY THE WHITE-FRONTED WOODPECKER IN THE MONTE DESERT, ARGENTINA¹

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Abstract. In the Monte desert of South America, the overall supply of water and food for birds decreases in the dry, cold season (June through September). During this period the White-fronted Woodpecker (*Melanerpes cactorum*) drills holes in the trunks and branches of *Prosopis flexuosa* and feeds on the exuded sap. Other bird species, diverse in ecological attributes and taxonomic affinities, take advantage of this resource which otherwise would be rarely available. Sap is a major constituent of the diet of the White-fronted Woodpecker and 11 other bird species, and sap feeding comprises between 16% to 83% of foraging observations made during June and July. Aggression by White-fronted Woodpeckers significantly reduced the time smaller bird species spent feeding on sap, indicating that White-fronted Woodpeckers actively compete for this resource. Other bird species profit from having access to a resource rich in water and sugar.

Key words: *Argentina, competition, facilitation, Melanerpes cactorum, Monte desert, sap feeding, White-fronted Woodpecker.*

Resumen. En el desierto del Monte de Sudamérica, la oferta de agua y alimento para las aves disminuye durante la estación seca de invierno (junio a septiembre). Durante este período, el Carpintero de los Cardones (*Melanerpes cactorum*) taladra los troncos y ramas de *Prosopis flexuosa* y se alimenta de la savia que

fluye de las perforaciones. Otras especies de aves, de diferentes grupos ecológicos y taxonómicos, aprovechan este recurso, que de otro modo raramente está disponible. La savia es un componente importante de la dieta del Carpintero de los Cardones y de otras 11 especies de aves; durante los meses de junio y julio constituye del 16% al 83% de las observaciones de forrajeo. La agresión por los Carpinteros de los Cardones reduce significativamente el tiempo de alimentación en las perforaciones con savia de las especies más pequeñas. En la explotación de este recurso se revela una compleja combinación de interacciones positivas y negativas entre las aves. Las interacciones agonísticas sugieren que el Carpintero de los Cardones compite activamente por este recurso, mientras que las otras especies de aves se favorecen al acceder a un recurso rico en agua y en azúcares.

In Europe and North America, several species of woodpeckers feed on the sap flowing from drilled holes (Foster and Tate 1966, MacRoberts and MacRoberts 1976, Short 1982). This behavior is perhaps best exemplified by the Yellow-bellied Sapsucker (*Sphyrapicus varius*). The sap from holes drilled by this species attracts, and is used by, other taxa including insects, birds, and mammals (Foster and Tate 1966, Wiens 1989, Holmes 1990). Use of this food resource may be particularly important to hummingbirds, because they require food of high energy content (Miller and Nero 1983).

In South America, two species of woodpeckers of the genus *Melanerpes* use sap as a food resource: the

¹ Received 26 January 1998. Accepted 30 September 1998.