Studies in Avian Biology No. 29:75–81

A EUROPEAN EXAMPLE OF STANDARDIZED MIST NETTING IN POPULATION STUDIES OF BIRDS

ANDREAS KAISER AND PETER BERTHOLD

Abstract. The "MRI-program" is a standardized long-term bird trapping program that has been in existence since 1974. Three central European stations are run daily during the entire autumn migratory period from June through November. Three other stations follow the same highly standardized protocol. In this paper, the field methods are described and standardization is discussed. Advantages of standardization include improved accuracy of capture–recapture estimates of population size and other parameters.

Key Words: capture–recapture, migrant, mist net, monitoring, MRI-program, passerine, standardization.

The standardized study of many different species and populations of birds at the same time, over broad geographic scales, offers valuable opportunities to monitor bird populations and at the same time study factors affecting population dynamics. Two examples of such projects that involve mist netting to capture birds are migration and stopover studies (Bairlein 1998, Bairlein and Giessing 1997, Bairlein et al. 1994), and productivity and survival studies (DeSante 1992, DeSante et al. *this volume*, Peach and Baillie *this volume*). Each of these programs uses highly standardized methods, both to reduce bias in sampling and to facilitate strong statistical analysis. Another example, described here, is the "MRI-program," which currently consists of up to six trapping sites in operation during fall (Fig. 1).

Long-term research programs were begun at three inland stations: the Mettnau peninsula in south Germany, the nature reserve "Die Reit" in north Germany near Hamburg, and in east Austria in the nature reserve at the eastern shore of Lake Neusiedl near Illmitz. Preliminary work was done in 1972 and 1973, and these sites have been run under standard conditions since 1974. Later additions included a banding site at lake Galenbeck in northeastern Germany, and two coastal sites, the Ebro-Delta banding site in Spain and Rybachy at the Kurish Split in Russia (Fig. 1). The latter two sites collaborate closely with the Vogelwarte Radolfzell.

Sites were chosen according to four criteria: (1) at least one site should sample each of the autumn migratory populations of central, northern, western, or eastern Europe, as shown by the atlas of songbird migration (Zink 1973–1985); (2) the stations should be situated in protected areas that would not be disturbed during long-term studies; (3) the areas should have a high degree of climax vegetation and thus show relatively few changes over the long term; and (4) the areas should be excellent bird conservation areas with rich bird life during the breeding season as well as the migration period. In addition to these considerations, the suitability of the areas was tested by sample trapping during the pilot years.

The program was designed so that a number of questions could be answered, including five main topics:

(1) *Population dynamics and demography*: Short-term and medium-term fluctuations in numbers of migrants, as well as long-term population

FIGURE 1. Banding sites of the Mettnau-Reit-Illmitz-program in Europe and sites in cooperation with the "Vogelwarte Radolfzell" (German bird-banding office). M=Mettnau (Lake Constance), RE=Reit (Hamburg), I=Illmitz (Lake Neusiedl, Austria), G=Galenbeck (Lake Galenbeck), RY=Rybachy (Rossitten, Russia), E=Ebro-Delta (Tarragona, Spain).

changes and their magnitudes, with a special focus on decline of small birds (Marchant 1992, Berthold et al. 1993, Böhning-Gaese 1995, Kaiser and Berthold 1995). Demographic studies were to look at age and sex differences and their role in migratory and stopover behavior, habitat preference, nutrition, and many other topics.

(2) *Migration*: Phenology of migration, migration routes, and strategies of migration and stopover (Berthold 1996, 2001). Also studied are the dependence of these features on sex, age, the breeding area and range of the populations, and seasonal and climatic factors. Finally, questions are investigated on migratory physiology, such as fat deposition, the control of migration, stopover behavior, and the interplay of molt, migration, and energy balance (Berthold et al. 1991; Kaiser 1992, 1993b, 1996).

(3) *Biorhythmicity*: Special attention is given to daily activity patterns of staging individuals, molt (Kasparek 1981), and to the variation in migration patterns from year to year (Bairlein 1981, Brensing 1989).

(4) *Ecosystem research*: Resource partitioning and utilization of stopover sites are of interest, including the role of habitat (Streif 1991), nutritional preferences (Brensing 1977, Grosch 1995), mobility (Bastian 1992), stopover period (Kaiser 1993b), population size and turnover (Kaiser 1995), and competition. Other studies investigate the carrying capacity of a stopover area for small birds and how such an area can be made optimal.

(5) *Methodological research:* Repeatability and observer bias in wing length measurements, fat scoring, and ageing techniques were studied (Berthold and Friedrich 1979; Kaiser 1993a, 1993b). Capture–recapture and other counting methods look at frequency and intensity of operations of the nets required to gain an adequate sample size.

In this paper, we discuss features of the MRI-program that are particularly relevant to population monitoring.

METHODS

The trapping site at Mettnau is typical of the operation of a single large-scale netting station in the MRI-program, and is described as an example. This site is an area of approximately 1 km^2, situated on the Mettnau Peninsula nature reserve east of Radolfzell at Lake Constance (Berthold et al. 1991). There are 52 mist nets in use, placed in a single transect through a *Phragmites* reed swamp, but sampling all habitat types characteristic of the peninsula (Streif 1991). Distance between nets and release (banding) site range from 55 to 360 m. Operations are run daily through the fall season (30 June–6 November). Nets are open 24 h. Nets are checked at fixed intervals over the entire day (hourly, except half-hourly in poor weather). No activity is permitted near nets between net checks, and all captures are passive (no chasing or tape lures).

As noted by Bibby et al. (1992), standardization in capture and census methods is needed to reduce bias, and all MRI procedures are highly standardized (Berthold and Schlenker 1975). The number of nets, net locations, hours of operation, timing of net rounds, sequence of checking nets, and height of shelf strings on each net pole are all constant from year to year. Also standardized are all instructions and materials (bands, color rings, balance, tools, rulers). Vegetation is cut back in the off-season to keep habitat and vegetation structure as stable as possible.

Data recorded in the MRI-program include the following:

(1) *Trapping status*: first capture, within-site retrap from the same season, retrap from previous years, or banded elsewhere in the same or an earlier season (foreign retrap). Retraps are handled like first traps except that retraps from the same season do not have wing and foot remeasured, and for same-day retraps, sex, age, and molt are skipped.

(2) *Band number*

(3) *Date*

(4) *Capture time*: time when the net was checked and the bird removed from net.

(5) *Program status*: indicates whether species are study targets (full data collected) or non-target (full data collected only if there is time). Up to 41 species are targets at each site, whereas there are up to 100 non-target species.

(6) *Species-code*: German or Latin abbreviation, or species number

(7) *Net, shelf, and side of net in which the bird was trapped*: net shelves counted from ground upwards, 1 to 4. Left or right of nets are marked by signs at each nets. Data are recorded on a slip of paper placed into the carrying bag for each bird.

(8) *Sex*: recorded only when accurately determinable; otherwise coded as undetermined

(9) *Age*: two age classes are defined: this-year birds (juveniles, yearlings) and adults (older birds, born in the previous calendar year or earlier). Age is recorded only if accurately determinable, for example, by skull pneumatization or by molt limits in the wing (Jenni and Winkler 1994); otherwise coded as unknown age.

(10) *Molt*: body molt is recorded using methods described by Berthold et al. (1970), whereas wing feather molt follows Berthold et al. (1991). Tail feather molt is not recorded.

(11) *Length of the third primary*: length of third wing feather (counting from the outside) gives a relative wing measure that is more convenient to measure than wing chord (Berthold and Friedrich 1979, Svensson 1992).

(12) *Special data for species identification*: notch of the second primary and foot span are measured, to allow discrimination of *Acrocephalus* species.

(13) *Fat class*: using methods of Kaiser (1993a).

(14) *Body mass*: weighed to the nearest 0.1 g within 1 h of capture, using an electronic balance.

RESULTS AND DISCUSSION

Here we discuss some results from the MRI-program that are relevant to the use of mist nets for monitoring, and that illustrate the value of standardization.

STANDARDIZATION

Our results have shown that different species, and different numbers of each species, are caught in different habitats (Bairlein 1981, Streif 1991, Mädlow 1994). Therefore, moving or changing the total number of nets within or between seasons will alter numbers captured and affect annual indices of abundance. In capture–recapture studies, more birds may be recaptured if nets are relocated frequently (see below), but this would alter the probability of capture and recapture in complex ways that would be very difficult to model in analyses. Only in standardized capture–recapture studies are basic model assumptions met and resulting estimates precise (Otis et al. 1978). We therefore recommend that a station should run with the same number of nets in exactly the same positions each year. For the same reason, it is important to prevent habitat change at the net sites, because habitat change affects capture–recapture probabilities in a manner analogous to moving nets among habitats.

With standard net locations, some species will have low capture probability because relatively little of their specialized habitat is sampled (e.g., Lesser Whitethroat, *Sylvia curruca*; Kaiser 1993b). It is therefore important to determine which species are the targets of study before determining where nets should be placed.

At the main MRI study site, the frequency of all first captures differed among habitats, but the proportions were fairly constant from year to year over a 22-year period (Fig. 2). However, capture indices decreased slightly in the four bushy habitats and increased in reed habitat C. To examine the effect of habitat change, we calculated species-specific long-term population trends separately for the birds

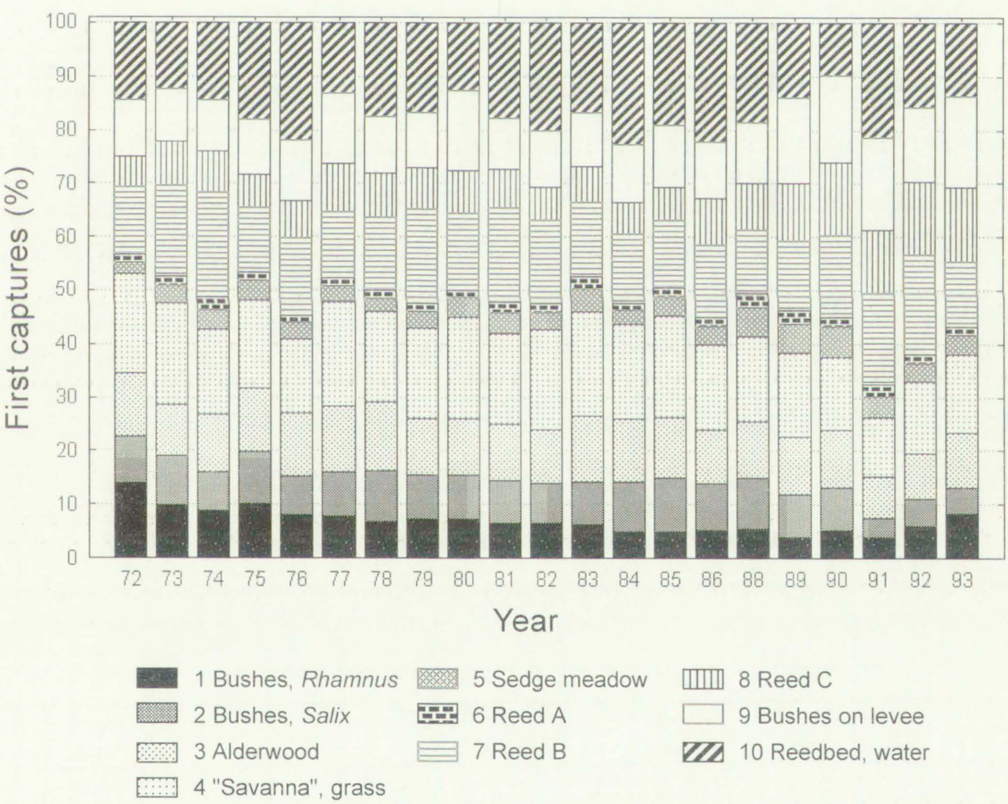

FIGURE 2. Percent of birds captured during June to November at Mettnau in different habitats and years. 1987 missing due to flood.

TABLE 1. LONG-TERM POPULATION TRENDS (1972–1993) FOR FIRST-CAPTURES IN DIFFERENT HABITATS AT METTNAU, GERMANY (KAISER AND BERTHOLD 1995)

	Habitat											
Species	1	2	3	4	5	6	7	8	9	10	All habitats	N
Wryneck (*Jynx torquilla*)	–	ns	–	ns	–	–	–	ns	ns	–	-0.65**	153
Wren (*Troglodytes troglodytes*)	-0.51*	-0.46*	ns	ns	ns	–	ns	ns	ns	-0.49*	ns	1,280
Dunnock (*Prunella modularis*)	ns	ns	-0.50*	ns	ns	–	ns	0.70*	0.62*	ns	ns	1,331
Robin (*Erithacus rubecula*)	-0.62*	ns	ns	0.56*	0.54*	0.60*	0.58*	ns	ns	ns	ns	9,619
Nightingale (*Luscinia megarhynchos*)	ns	ns	ns	ns	–	–	–	–	ns	–	0.52*	219
Bluethroat (*L. svecica*)	–	–	–	–	ns	–	ns	ns	–	ns	-0.44*	177
Black Redstart (*Phoenicurus ochruros*)	ns	ns	0.45*	ns	ns	–	ns	ns	0.48*	ns	ns	516
Redstart (*P. phoenicurus*)	-0.67*	-0.60*	-0.70**	-0.78**	ns	–	ns	ns	-0.56*	-0.54*	-0.77**	939
Whinchat (*Saxicola rubetra*)	–	–	–	–	-0.64*	ns	ns	ns	–	ns	-0.47*	277
Blackbird (*Turdus merula*)	ns	ns	ns	ns	ns	–	ns	-0.64*	ns	ns	ns	2,379
Song Thrush (*T. philomelos*)	0.46*	ns	ns	ns	ns	–	ns	ns	ns	ns	ns	1,654
Grasshopper Warbler (*Locustella naevia*)	-0.52*	-0.47*	ns	ns	ns	ns	-0.59*	ns	ns	ns	-0.69**	1,087
Savi's Warbler (*L. luscinioides*)	–	–	–	–	–	–	ns	ns	–	ns	ns	144
Aquatic Warbler (*Acrocephalus paludicola*)	–	–	–	–	ns	–	ns	–	–	–	-0.72**	49
Sedge Warbler (*A. schoenobaenus*)	–	–	–	–	ns	ns	-0.66*	ns	ns	ns	-0.49*	1,333
Marsh Warbler (*A. palustris*)	0.89*	ns	-0.80**	-0.54*	ns	ns	-0.84**	ns	-0.49*	-0.56*	-0.77**	1,435
Reed Warbler (*A. scirpaceus*)	-0.73**	-0.58*	-0.51*	-0.72*	ns	0.49*	-0.45*	0.74**	ns	ns	ns	39,309
Great Reed Warbler (*A. arundinaceus*)	–	–	–	–	–	–	-0.65*	ns	ns	-0.64*	-0.75**	329
Icterine Warbler (*Hippolais icterina*)	-0.60*	ns	ns	ns	–	–	ns	–	ns	–	ns	580
Lesser Whitethroat (*Sylvia curruca*)	-0.65*	-0.55*	-0.60*	-0.75**	–	–	ns	ns	-0.47*	ns	-0.79**	2,235
Whitethroat (*S. communis*)	ns	ns	ns	ns	–	ns	ns	ns	ns	ns	ns	456
Garden Warbler (*S. borin*)	-0.68**	-0.56**	-0.46*	ns	0.49*	–	0.67**	ns	ns	0.49*	ns	9,579
Blackcap (*S. atricapilla*)	-0.45*	ns	ns	ns	0.86**	ns	0.70**	0.60*	0.71**	0.50*	0.43*	13,615
Wood Warbler (*Phylloscopus sibilatrix*)	–	–	–	ns	–	–	–	–	ns	–	-0.62**	72
Chiffchaff (*P. collybita*)	-0.72**	ns	-0.43*	-0.60*	ns	ns	0.46*	ns	ns	ns	ns	17,608
Willow Warbler (*P. trochilus*)	-0.86**	-0.82**	-0.64*	-0.83**	ns	ns	ns	ns	ns	ns	-0.81**	7,419
Goldcrest (*Regulus regulus*)	ns	0.55*	ns	0.53*	–	–	–	–	–	–	ns	451
Firecrest (*R. ignicapillus*)	ns	ns	ns	ns	–	–	–	–	–	–	ns	184
Spotted Flycatcher (*Muscicapa striata*)	ns	ns	ns	-0.60*	ns	–	ns	ns	ns	ns	-0.60**	807
Pied Flycatcher (*Ficedula hypoleuca*)	ns	ns	ns	ns	ns	–	–	–	ns	–	ns	656
Blue Tit (*Parus caeruleus*)	-0.60**	ns	ns	-0.52**	ns	ns	ns	ns	ns	ns	-0.44*	5,563
Red-backed Shrike (*Lanius collurio*)	–	–	–	ns	–	–	ns	ns	ns	–	-0.49*	153
Goldfinch (*Carduelis carduelis*)	-0.66*	ns	ns	ns	–	–	–	ns	ns	–	ns	481
Bullfinch (*Pyrrhula pyrrhula*)	-0.56*	ns	ns	0.52*	–	–	–	–	–	–	ns	999
Reed Bunting (*Emberiza schoeniclus*)	ns	ns	ns	-0.52*	-0.45*	ns	-0.48*	ns	ns	ns	ns	7,960
All species combined	-0.76**	-0.60*	-0.57*	-0.55*	ns	ns	ns	0.50*	ns	ns		130,478

Notes: Trends are coefficients of annual capture totals linear regressed on year. See Fig. 2 for definition of habitats.
* denotes $P < 0.05$; ** denotes $P < 0.001$; ns denotes $P > 0.05$.

captured in each habitat. Differences in trend among habitats would suggest that habitat change has been taking place over time. For the most part, the trends were very consistent within species among habitats (Table 1). However, in the habitat with dense bushes of buckthorn (habitat 1), the Garden Warbler (*Sylvia borin*), Blackcap (*S. atricapilla)*, Robin (*Erithacus rubecula*), and Bullfinch (*Pyrrhula pyrrhula*) were decreasing and the Marsh Warbler (*Acrocephalus palustris*) was increasing, whereas in other habitats population trends of these species were in opposite directions. The Chiffchaff (*Phylloscopus collybita*) showed negative trends in some habitats, but a positive trend in reed B (Table 1). Other species were also captured in remarkably high numbers in later years in reed habitats, and this may be related to an increase in the number of buckthorn bushes within the reed. These results illustrate the importance of maintaining habitat at the same stage over time.

Another possible reason for change in the numbers of birds captured in each habitat could be changes in food abundance, such as fruit patterns related to the height of mist nets or outbreaks of insects in particular habitat types. This kind of variation cannot be controlled with habitat management, but food abundance is not expected to change in a systematic way over time, so long-term trends should be unbiased by this variation.

Timing of operations should be standardized, as well as number and location of nets. Data collected both during migration (Brensing 1989) and during the breeding period (A. Kaiser, unpubl. data) show a strong peak in the number of captures early in the morning, and a second (much lower) peak before dusk. Equal net-hours each day are not equivalent, therefore, unless those net-hours are from the same portion of each day (Karr 1981a). Expressing total number of birds captured as birds/net-h is therefore an ineffective way of controlling for variation in effort, and the schedule of netting operations should instead be standardized.

Relative Abundance

To test the efficiency and accuracy of mist nets for species inventory and estimates of relative abundance, we compared mist-net counts with different counting methods during the main breeding period from May to July. During this period, population size of adults can be assumed to be relatively constant. At an isolated study plot in south Germany near Espasingen we used a net density of 35-m net/ha in a 9-ha site (and 45-m net/ha in a nearby site of 3 ha), and achieved high capture (and recapture) probabilities. The correlation between number of all species of breeding birds detected by mist-net captures (first captures only) and point counts was strongly positive ($r = 0.83$, $P < 0.001$), but netting totals were nearly always higher than point count totals (Fig. 3; Kaiser and Bauer 1994). The study suggested that netting can be used to sample a consistent percent of a population (although that percent may differ widely among species). Mist-net captures may therefore be a particularly good means of sampling migrants, because it takes place over many hours (unlike transect or point counts) and does not require birds to be singing for them to be detected.

Population Trends

The length of a long-term population monitoring project should be at least 15–20 years to cover natural population fluctuations (Berthold and Querner 1978, Tucker and Heath 1994). Analyses of first capture data from the MRI-program for long term trends have been published regularly (Berthold et al. 1993, Kaiser and Berthold 1995, Berthold *this volume*). Böhning-Gaese (1995) determined that species with similar year-to-year population fluctuations do not necessarily have similar long-term trends. Moreover, results of small-scale study on migration season population trends cannot be taken to represent population change on larger spatial scales in the absence of information on which breeding population is being sampled at the migration station (see Dunn and Hussell 1995).

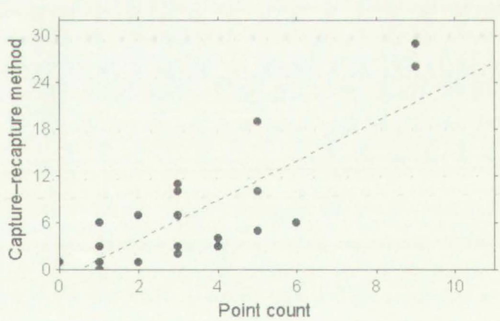

FIGURE 3. Number of local breeders captured (calculated from the number of adult first captures divided by 2 for an estimate of "pairs") compared to point count estimates at a woodland near Espasingen, Germany during the breeding period 1992 (Kaiser and Bauer 1994). Each point represents one species. Linear regression, $r = 0.83$, $R^2 = 0.70$, $P < 0.001$, $N = 29$.

Capture–recapture Studies: Breeding Season

Capture–recapture data are affected by net avoidance by birds that have already been captured once (Kaiser 1995). Recapture rate is generally much lower than expected when trapping is frequent (Buckland and Hereward 1982), although some species do not change their behavior drastically after the first catch. The extent of bias can sometimes be tested using mathematical models. We suggest two types of behavioral response to mist netting: (1) if many nets are used in comparison to the size of the study site, most birds learn to avoid the nets; and (2) intensive netting can cause too much direct human disturbance, causing birds to leave the area. These predictions have to be tested further, for example, in combined capture–recapture and telemetry studies.

In the breeding season, leaving up to 6 days between netting sessions increased capture and recapture rates (Dorsch 1998). One strategy for reducing net avoidance (other than reducing netting frequency) is to change net locations, but this compromises standardization (see above). Despite the problem of net avoidance, the MRI-program continues with daily netting in fixed locations, in part because net avoidance is a smaller problem with migrating birds (see below), and because our main objective is to analyze patterns of first captures under standard conditions.

Mist-net samples do not capture all the birds present, and capture–recapture models can be used to determine total population size. For example, in a study of a Reed Warbler (*Acrocephalus scirpaceus*) population at Lake Galenbeck, 254 adult Reed Warblers were caught at least once, with a total of 106 retraps (Fig. 4). Program CAPTURE (Otis et al. 1978) was used to estimate population size. The appropriate time effects and behavioral response model (White et al. 1982) estimated a population size of 500 birds, and the average estimate of all models was 430 (Fig. 5).

Capture–recapture Studies: Migration Season

Population size estimates during the migration period are more difficult to calculate than for breeding populations, because a set of well-defined assumptions of models for open population are violated and recapture numbers are not high (Kaiser 1995). To optimize sampling, density and distribution of nets is important. To obtain more recaptures, their density and distribution has to be adapted to the behavior of passerines stopping over. The interaction between capture behavior, recapture probability, disturbance,

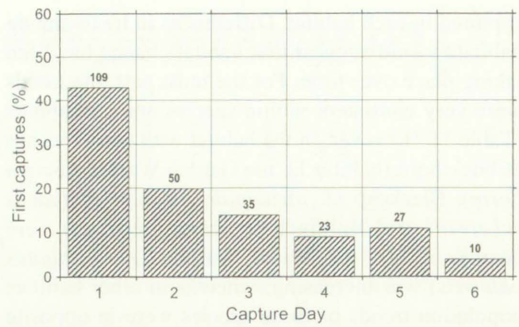

FIGURE 4. Decline in number of first captured Reed Warblers during the first 6 d of the MRI-program, i.e., at the end of the breeding period, at Lake Galenbeck, Germany.

and other biases (Pollock et al. 1990) was discussed by Kaiser (1993b, 1995).

During migration seasons, there is high turnover in individuals present (as shown by the low proportion of retraps), so number of first-time captures is increased by daily netting, and there are few birds stopping over that will develop net shyness (Kaiser 1993b). Nonetheless, Dorsch (1998) has shown that net avoidance may also be an issue with birds that are spending many days at a stopover site. Recapture probabilities during migration must be especially high (>0.2) to estimate other parameters, such as body mass change in relation to capture behavior. At some sites this is feasible, as shown by the 36% retrap rate obtained during 1988–1989 at the Mettnau Peninsula (Kaiser 1995).

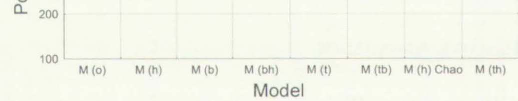

FIGURE 5. Number of breeding Reed Warblers estimated with different models of program CAPTURE (Otis et al. 1978). Capture probabilities are constant in model M_o, or vary by time (M_t), due to behavioral response (M_b), by individual birds (M_h), or by two sources of variation in its capture probabilities (M_{tb}, M_{th}, M_{bh}). Data from Lake Galenbeck, Germany, 1991 and 1992. Point estimates (means) with standard error. Number of first captures was 254, and mean populations size of all models 430.

Mobility of stopover populations was studied by examining the exchange rate of individual birds captured at five banding sites at the Mettnau peninsula during the migration period (Kaiser 1995). With knowledge of the exchange rate, an estimate of the size of the stopover population in the isolated nature reserve was derived from Jolly-Seber estimates. True average stopover time was estimated at 16 days, and it was shown that there were temporal behavioral responses to mist netting and ringing. Nonetheless, variation in capture probability was detected in birds according to differences in body condition, molt, mobility, and behavioral response to mist netting (Kaiser 1993b, 1995). The release of birds at the processing site, up to 500 m away from the trapping site, might affect retrap probabilities by causing the bird to shift its center of activity. Lastly, social interactions, like territorial defense, have an influence on recapture probabilities. All these potential problems should be investigated in further studies. Nonetheless, the capture design chosen in the MRI-program has given clear results for questions of migration patterns, habitat use, and condition of first captures (Berthold et al. 1991, Kaiser 1996).

ACKNOWLEDGMENTS

We thank C. D. Otahal, C. J. Ralph, and L. Thomas for their helpful comments on the manuscript. This final version greatly improved due to the critical input of E. H. Dunn.