J. Field Ornithol., 67(2):263–274

CAPTURE EFFICIENCY OF MIST NETS WITH COMMENTS ON THEIR ROLE IN THE ASSESSMENT OF PASSERINE HABITAT USE

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Abstract.—Variation in capture efficiency of mist nets among species or with weather and habitat may affect the interpretation of mist-netting data for studies of habitat use and diurnal activity. Capture efficiency of mist nets with a mesh size of 36 mm was determined by observing birds flying towards the nets in various habitats (reed-bed, bushes, grassland). The proportion of birds escaping from a mist net shelf after having entered it depended on the size of the species and on wind speed. Small passerines and species as large as thrushes or larger escaped more frequently than intermediate-sized passerine species of 10–25 g. Strong winds added 7–16% to the escape rates under weak winds. The proportion of birds avoiding mist nets without entering a shelf depended on the degree of shading and net-shelf height, but not on species, wind speed, and habitat. Birds flying towards mist nets in full sunlight or towards the top shelf avoided the net more frequently than birds flying towards partially or completely shaded mist nets or towards lower net shelves. We conclude that capture frequencies from mist netting are an adequate method for assessing habitat use of small birds, but with certain reservations: capture numbers do not represent quantitatively the species composition and all mist nets should be similarly exposed to the sun and wind (i.e., preferably in a straight line in vegetation as high as the nets).

EFICIENCIA DE CAPTURA DE LAS REDES SEMITRANSPARENTES CON COMENTARIOS SOBRE SU ROL EN EVALUAR EL USO DE HÁBITAT POR PASERINOS

Sinopsis.—La variación en la eficiencia de captura de redes semitransparentes entre especies o con el tiempo y el habitat pueden afectar la interpretación de los datos de estudios con redes para uso de habitat y de patrones de actividad diurna. La eficiencia de captura en redes con un tamaño de malla de 36 mm se determinó observando aves volando las redes en varios hábitats (cama de cañas, arbustos, yerbazales). La proporción de aves escapando de las redes una vez habian entrado a ella depende del tamaño de la especie y de la velocidad del viento. Paserinos muy pequeños y especies del tamaño de Turdidos o mayores escaparon más fecuentemente que pequeñas especies paserinas de 10–25 g. Vientos fuertes añadieron otros 7–16% a las tasas de escape bajo condiciones de vientos leves. La proporción de aves evitando las redes sin entrar a ellas dependió de el grado de sombra y altura de las estratas, pero no en especies, velocidad del viento ni habitat. Aves volando hacia las redes en plena luz solar o hacia la estrata superior de estas evitaron la red más frecuentemente que aves volando hacia redes parcial o totalmente sobreadas o hacia la estratas bajas de las redes. Se concluye que las frecuencias de captura en las redes son un método adecuado para evaluar el uso de habitats por aves pequeñas, pero con ciertas reservas: los números de captura no representan la composición de especies cuantitativamente; todas las redes debían estar expuestas al sol y al viento de forma similar, i.e., preferiblemente en una línea recta en vegetación tan alta como las redes.

Small birds living in dense vegetation are usually difficult to census, especially outside the breeding season. Therefore, techniques other than observational and aural census methods have to be used. Standardized mist netting is among the most efficient of such techniques (Berthold 1976, Karr 1981), and several long-term projects currently use this method (e.g., Baillie 1990, Berthold and Schlenker 1975). These studies aim to assess quantitatively the spatial and temporal distribution of small birds or to estimate their relative numbers. The advantages and disadvantages of mist netting for estimating relative densities of birds in space or time have been evaluated (reviewed in Berthold 1976; Karr 1979, 1981). A prerequisite for such studies is that mist netting is standardized as much as possible by setting a constant number of nets of the same type in the same place for the same length of time, using regular net rounds, and constant daily opening hours (Berthold 1976, Berthold and Schlenker 1975).

An aspect that has received less attention is that the accuracy of density estimates depends critically on the variation in capture efficiency among habitats, times of day, and species. There are few published studies of capture efficiency, which has been shown to depend on the type of mist net used (e.g., mesh size, tethered or not, color) and on weather (Dorsch 1983; Heimerdinger and Leberman 1966; Karr 1979, 1981; Pardieck and Waide 1992). To our knowledge, there is only one study that investigated whether capture efficiency varied among habitats (Bairlein 1981). This study showed that variation in capture efficiency among nets within the same habitat was relatively small, but was larger between habitats, perhaps as a result of a concomitant change in species composition. Unfortunately, the species and the weather were not taken into account in that study.

The aim of this study, therefore, was to investigate in more detail the effect of species, habitat, and weather on capture efficiency, and thereby on mist-net studies of habitat use and diurnal activity.

METHODS

In this study, capture efficiency of mist nets is defined as the proportion of birds taken out of the mist net by the observer (C) out of the total of birds flying towards the mist net (T), i.e., those birds that would have been caught if none of the birds had reacted to the net. The birds not handled by the observer ($T - C$) can be subdivided into those avoiding the net during flight (A) and those escaping after entering a shelf (E). Hence, the total number of birds that would have been handled by the observer if birds were not reacting to mist nets at all is described by the function $T = A + E + C$.

Mist nets were observed at a banding site at Lake Neuchâtel near Estavayer-le-Lac, Switzerland (46°52′N, 6°52′E), where mainly migrants during stopover were caught, and at the Alpine pass Col de Bretolet, Switzerland (46°09′N, 6°47′E), where mainly diurnal migrants during active migratory flight as well as migrants landing in bushes were caught. All mist nets were black, 9-m or 6-m long, 2-m high, had four shelves, a mesh size of 36 mm, and were tethered on the top.

Nets were placed in a straight line in five more or less homogeneous habitats: (B) bushes of about 3-m height (Lake Neuchâtel, four nets of 9 m); (R) reed-bed of about 3-m height (Lake Neuchâtel, five mist nets of 9 m); (S) open area covered with sedges (0.5-m high) and small bushes (2-m high) (Lake Neuchâtel, five nets of 9 m); (A) green alder bushes (*Alnus viridis*) of 2–3-m height at the top of the pass (Col de Bretolet, six nets of 6 m); (G) grassland at top of the pass (Col de Bretolet, three nets of 9 m on level ground and six nets of 6 m on a ridge). In addition, six double nets consisting of two 6-m nets, one above the other, were placed parallel to the row of normal mist nets. The lower net spanned the heights 2–4 m; the upper net reached from 4–6 m. All of these nets were easily visible against the sky.

Observations at Lake Neuchâtel took place 24 August–4 September in the morning and afternoon: 11 d (52 h) for habitat B, 12 d (60 h) for R, and 6 d (18 h) for S. At the alpine pass Col de Bretolet (habitats A and G), observations took place at irregular intervals on 12 d during 15–26 September and 1 October. During each observation period, wind speed (Beaufort scale: no wind = Beaufort 0–1, slight = Beaufort 2, moderate = Beaufort 3, strong = Beaufort 4–5) and the shading of the net (full sun, partially shaded, completely shaded by vegetation or clouds) was recorded.

Observers hid in a blind at one end of the mist net row and classified the birds flying towards the nets as: birds avoiding the mist net in flight or touching the mist net, but not entering a shelf (A); birds entering a shelf and escaping (E); birds entering a shelf and being taken out by another observer at regular hourly net rounds (C). Observers also recorded the net shelf towards which the birds flew (on Col de Bretolet for only 161 out of 263 birds) and, if possible, the species (123 unidentified out of 661 birds).

For the analysis of the proportion of birds escaping from a mist net shelf after having entered it, $E/(C + E)$ was calculated. To analyse the effects of habitat and weather on the avoidance of mist nets, A/T was used. Two-way contingency tables were tested for interactions by chi-squared test of independence (with Yates correction, where appropriate). Higher order contingency tables were analyzed with hierarchical log-linear models with backward elimination of non-significant interaction terms (procedure hiloglinear of the statistical package SPSS/PC+, Norusis 1988).

An additional data set was available on birds escaping from mist net shelves. It consisted of the proportion of birds escaping from shelves observed during regular hourly net rounds during a one-year study with 180 m of mist nets in a riparian area at Lago Maggiore (46°09′N, 8°48′E), Switzerland, open 2 d/wk. The type of mist net used was the same as at the other two sites. These data do not provide absolute proportions of birds escaping from mist net shelves, because only those that have been observed escaping during the net rounds were recorded.

Species-specific escape rates were related to body length (total length minus tail and bill length; data from Cramp 1977), skull width (largest width; data from Cuisin 1989, data of woodpeckers from Natural History Museum, Basel) and body mass (data from Cramp 1977, given for central Europe).

RESULTS

Proportion of birds escaping from mist net shelves.—Data on escape rates from Lake Neuchâtel and Col de Bretolet covered only small passerines. At Col de Bretolet, a range of wind speeds occurred from almost none to strong winds. At this site, the proportion of birds escaping was low for light to moderate wind speeds (no wind, 9.1%, $n = 11$; slight wind, 7.7%, $n = 26$; moderate wind 10.5%, $n = 38$) but was significantly higher under strong winds (30.5%, $n = 82$). The low wind speeds encountered at Lake Neuchâtel had no significant effect on escape rates (no wind, 40.6%, $n = 69$; slight wind, 39.8%, $n = 171$). As data on certain species were only available from days with strong winds, escape rates were analyzed separately for low to moderate wind speeds and for strong winds.

Under low to moderate wind speeds, escape rates were high (29–46%) for Eurasian Reed (*Acrocephalus scirpaceus*), Sedge (*A. schoenobaenus*) and Willow Warbler (*Phylloscopus trochilus*) and low for all the remaining species (7%, $n = 116$). Those species with a sample size of seven or more were used for analysing relationships between escape rates and body length, body mass, or skull width. A significant linear relationship was found with body mass ($b = -2.27$, $r^2 = 0.49$, $P = 0.04$), but not with body length ($b = -0.78$, $r^2 = 0.16$, $P = 0.28$). The best relationship occurred with skull width, which separated the three warbler species with high escape rates from the other species (Fig. 1). From a multiple regression analysis, including the two wind speed classes as a dummy variable and from data on Hedge Accentor (*Prunella modularis*) and Chaffinch (*Fringilla coelebs*), which were observed under both weak and strong winds (Fig. 1: numbers 5a,b and 7a,b), it appeared that strong winds added another 7–16% to the escape rates under weak winds.

Although most birds escaped from the shelves immediately, some, especially Eurasian Reed Warblers, escaped after having been in the net up to 40 min. They apparently managed to slip through the mesh.

Data from Lago Maggiore covered a wider range of bird sizes from small passerines to birds as large as Eurasian Jay (*Garrulus glandarius*) and woodpeckers. The proportion of escapes from net shelves observed during regular hourly net checks was high for two particularly small species Winter Wren (*Troglodytes troglodytes*) and Eurasian Penduline Tit (*Remiz pendulinus*), as well as for all species larger than European Starling (*Sturnus vulgaris*) and thrushes (*Turdus* sp.). By fitting a reciprocal model to the data, significant relationships between escape rates and body length, skull width, or body mass occurred (body length: $r^2 = 0.60$, $F = 14.5$, $P < 0.001$; skull width: $r^2 = 0.54$, $F = 11.5$, $P < 0.001$). The highest correlation coefficient was found with body mass (Fig. 2), but the relationships with body length or skull width were not significantly weaker.

Avoidance of mist nets within habitats.—Firstly, we analyzed whether the

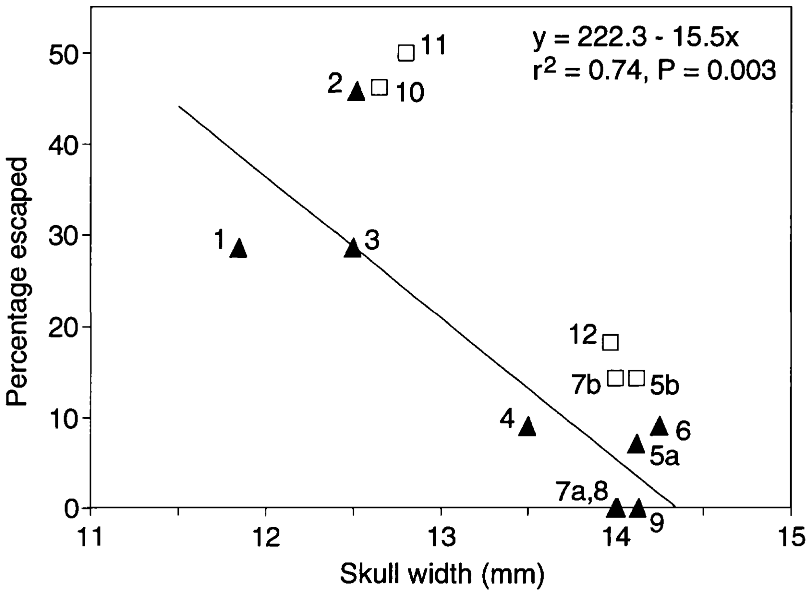

FIGURE 1. Percentage of birds escaping from mist net shelves at Lake Neuchâtel and Col de Bretolet versus skull width. Triangles = birds caught during low and moderate wind speeds with regression line. Open squares = birds caught during strong winds. 1 = *Phylloscopus trochilus* (n = 7), 2 = *Acrocephalus scirpaceus* (155), 3 = *A. schoenobaenus* (7), 4 = *Parus ater* (11), 5 = *Fringilla coelebs* (5a n = 28; 5b n = 28), 6 = *Erithacus rubecula* (11), 7 = *Prunella modularis* (7a n = 7; 7b n = 13), 8 = *Sylvia atricapilla* (12), 9 = *S. borin* (19), 10 = *Carduelis spinus* (13), 11 = *Motacilla flava* (10), 12 = *Anthus trivialis* (11).

proportion of birds avoiding mist nets differed between nets placed in the same habitat and whether it was related to wind speed and degree of shading.

Within habitats B, R and A, there were no significant differences in the avoidance rates among individual mist nets (chi-squared test of independence: habitat B: df = 3, P = 0.22; habitat R: df = 4, P = 0.70; habitat A: df = 4, P = 0.90). The six high nets in the open habitat G with an avoidance rate of 50% (n = 50) were not avoided significantly more frequently than the two groups of normal mist nets in the same habitat with avoidance rates of 55% (n = 20) and 38% (n = 56), respectively (chi-squared test of independence: df = 2, P = 0.28). For habitat S, sample sizes were too small for an analysis of individual nets.

Within each habitat, sunlight increased the avoidance rates, but not always significantly (Fig. 3). Wind speed had no significant effect on mist net avoidance, except in habitat A. There, the avoidance rate was significantly lower under moderate wind speed than under weak and strong winds. This difference was due entirely to the fact that all observations under moderate winds occurred when the nets were in the shade, whereas

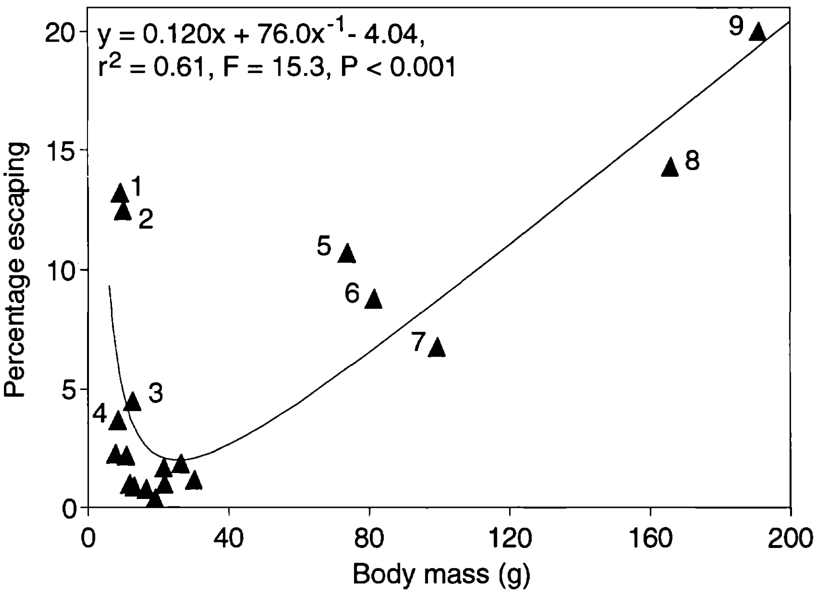

FIGURE 2. Percentage of birds observed escaping from mist net shelves during regular net rounds at Lago Maggiore versus mean body mass for 19 species. 1 = *Troglodytes troglodytes* (n = 38), 2 = *Remiz pendulinus* (8), 3 = *Acrocephalus scirpaceus* (223), 4 = *Aegithalos caudatus* (27), 5 = *Dendrocopos major* (28), 6 = *Sturnus vulgaris* (34), 7 = *Turdus merula* (429), 8 = *Garrulus glandarius* (7), 9 = *Picus viridis* (5), other species (0.4–2.5%) are *Erithacus rubecula* (374), *Phylloscopus* sp. (708), *Ficedula hypoleuca* (199), *Parus caeruleus* (89), *Passer domesticus* (81), *Passer montanus* (198), *Fringilla coelebs* (177), *Carduelis chloris* (54), *Carduelis spinus* (223), *Emberiza schoeniclus* (264).

observations under weak and strong winds mainly happened when nets were in sunlight. Within each habitat, log-linear models revealed no higher order interactions of mist net, degree of shading, and wind speed on the avoidance rates.

Birds flying towards the highest mist net shelf managed to avoid the net more often than birds flying towards lower shelves within each habitat (Fig. 4).

Avoidance of mist nets between habitats.—As there were no significant differences in avoidance rates among individual mist nets within the same habitat, data from the same habitat were pooled. In the log-linear model of the four-way contingency table of birds in each category of avoidance (yes/no), habitat, degree of shading (shaded, partially shaded, or completely in sunlight) and wind speed (none or slight/moderate or strong), only the two-way interaction between avoidance and degree of shading (partial χ^2 = 24.1, $P < 0.001$) was significant. The two-way interactions between habitat and degree of shading, habitat and wind, and degree of shading and wind were also significant ($P < 0.001$ for each), but are not of interest here. The interaction between habitat and avoidance (partial

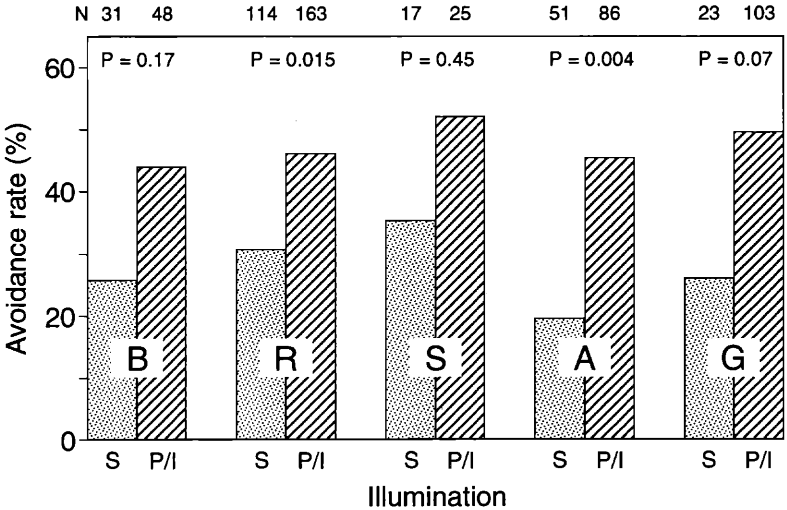

FIGURE 3. Avoidance rates for shaded (S) and partly or completely illuminated (P/I) mist nets in the five habitats B, R, S, A, and G. Numbers above the columns denote sample sizes. The significance level of the chi-squared test of independence for differences among illumination classes is given for each habitat.

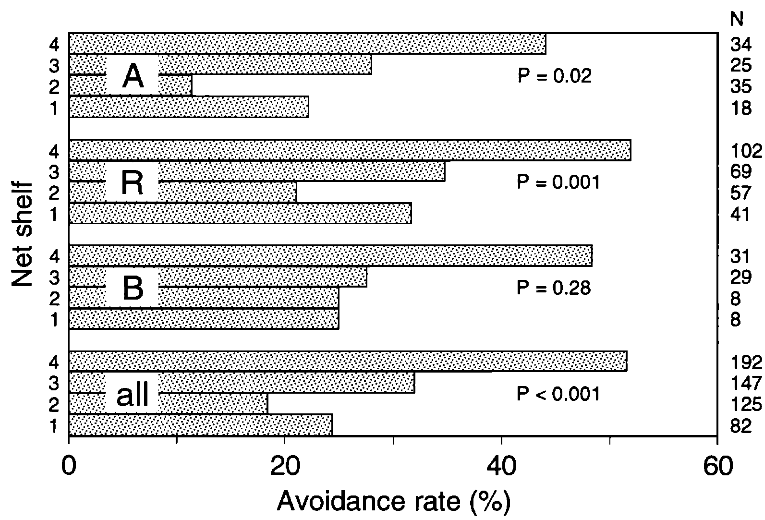

FIGURE 4. Avoidance rates of birds flying towards one of the four mist net shelves in the three habitats B, R, and A as well as for all habitats including data from habitats S and G. Numbers denote sample sizes. The significance level of the chi-squared test of independence for differences among shelves is given for each habitat. Net shelves are numbered from bottom (1) to top (4).

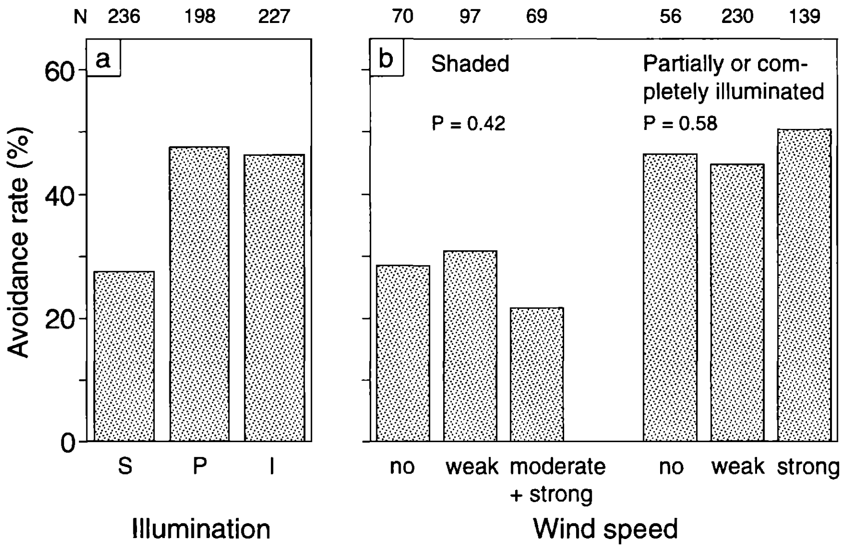

FIGURE 5. Avoidance rates for shaded (S), partially (P), or completely illuminated (I) mist nets (a) and for mist nets under different wind speeds (b) with significance level of the chi-squared test of independence. Numbers above the columns denote sample sizes.

$\chi^2 = 2.3$, $P = 0.68$, before backward elimination) and between wind speed and avoidance (partial $\chi^2 = 0.03$, $P = 0.87$) were not significant. Hence, although the open habitats S and G showed slightly higher avoidance rates, there were no significant differences in avoidance rates between habitats (Fig. 3). Avoidance rates were increased to a similar extent in both partially shaded and completely illuminated nets (Fig. 5a). Wind speed had no significant effect on avoidance rates (Fig. 5b).

Again, birds flying towards the top shelf managed to avoid the net more easily than birds flying against lower shelves (Fig. 4, $\chi^2 = 43.1$, df = 3, $P < 0.001$).

Avoidance of mist nets among species.—Species or groups of species with sufficiently large sample sizes were analyzed for interspecific differences in avoidance rates (Fig. 6). As the majority of unidentified birds avoided the nets, the unidentified birds were assigned to the most common species of the respective habitat. This is the Eurasian Reed Warbler in habitat R and S (86% of the identified birds) and the two *Sylvia* warblers in habitat B (64% of the identified birds). In habitat A and G, there were only three unidentified birds, which were omitted. To assign unidentified birds to the most common species is justified in this particular case by the fact that identification problems occurred only between species of similar shape in bad light (Eurasian Reed and Sedge Warbler, the latter representing only 3% of all identified birds in habitat R and S; Blackcap *Sylvia atricapilla* and Garden Warbler *S. borin* which were combined in Fig. 6).

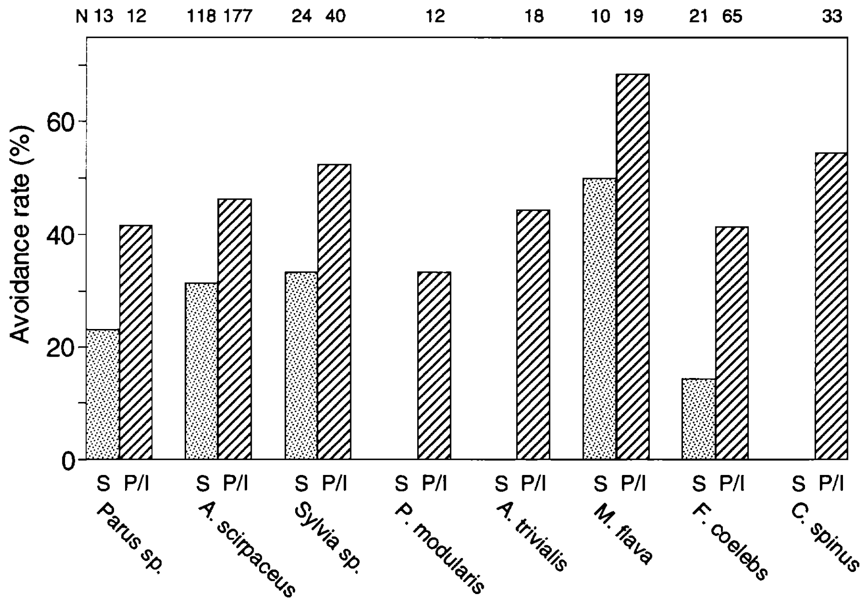

FIGURE 6. Avoidance rates of species or groups of species for shaded (dotted bars) and partly or completely illuminated (hatched) mist nets. *Parus* sp. = *Parus major, P. caeruleus, P. ater, P. cristatus; A. scirpaceus* = *Acrocephalus scirpaceus* and unidentified birds in habitats R and S; *Sylvia* sp. = *Sylvia atricapilla, S. borin* and unidentified birds in habitat B; *P. modularis* = *Prunella modularis; A trivialis* = *Anthus trivialis; M. flava* = *Motacilla flava; F. coelebs* = *Fringilla coelebs; C. spinus* = *Carduelis spinus.*

Degree of shading decreased the avoidance rate of all species, but avoidance rates were not significantly different between species for shaded ($\chi^2 = 4.9$, df = 4, $P = 0.30$) and partially or completely illuminated ($\chi^2 = 6.6$, df = 7, $P = 0.47$) nets (Fig. 6).

DISCUSSION

Effect of species.—Bird species had a large effect on capture efficiency, but affected only the escape rate from mist net shelves, and not the avoidance of nets. Escape rates of birds entering a mist net shelf primarily depended on the size of the species (Figs. 1 and 2). By increasing mesh size, the species caught are larger on average (Dorsch, 1983, Heimerdinger and Leberman 1966, Pardieck and Waide 1992). Therefore, it is probable that the diameter of the head and bird relative to mesh size contributes to whether a bird remains in the net shelf or not, i.e., whether a bird can slip through the mesh, whether the head is caught in the mesh, or whether the head cannot enter the mesh. This may also explain why body length of similarly sized passerines (data from Lake Neuchâtel and Col de Bretolet) is less important in explaining escape rates than body mass and skull width. In addition, large birds with larger feet and wings might more easily walk and flutter in the net and eventually jump out. Additional factors determining escape rates, not quantified in this study, may be the behavior of the bird in the net and the size and shape of the legs, feet, claws, wings, and tail.

Avoidance rates did not vary significantly among the species investigated (Fig. 6). The slightly higher avoidance rates of Tree Pipit (*Anthus trivialis*), Yellow Wagtail (*Motacilla flava*), and Eurasian Siskin (*Carduelis spinus*) may be a result of their migration in flocks. Birds following another bird flying into a net might react immediately and avoid the net more easily. There are certainly species not investigated in this study that are well known for their avoidance of mist nets, such as swifts.

Effect of weather.—Both wind and shade by vegetation or clouds affected capture efficiency. Whereas wind affected escape rates, degree of shading affected avoidance rates. Wind evidently helps birds in jumping out of the net by bagging the shelves. Apparently, wind did not increase the visibility of the nets to the birds. Visibility was certainly affected by direct sunlight which renders the nets slightly glossy. There are other weather factors that were not studied (e.g., rainfall). It is well known that few birds are caught during rain. It remains to be studied, however, whether this effect is due entirely to reduced locomotor activity or partly to water drops making the nets more visible.

Effect of habitat.—This study covered a wide range of habitats from bushes and reed-beds to grassland on top of a mountain ridge where the nets were clearly visible against the sky. Contrary to our expectation, avoidance rates did not differ significantly among habitats. When recording net avoidance, however, we considered the flight path to be only some meters in front of the net. Birds that recognized mist nets at a greater distance could not be judged reliably for avoidance behavior. From our own observations, it is likely that more birds make a more wide detour around mist nets in open than in closed habitats.

As nets in open habitats are usually more exposed to direct sunlight and wind than those in closed habitats, the degree of shading and wind may produce differences in capture efficiency among habitats. In many cases, such effects are difficult to separate from weather-dependent shifts in habitat use. As an example, the distribution of the European Robin (*Erithacus rubecula*) over a range of habitats at another banding site at Lake Neuchâtel is given for calm and windy days in Fig. 7. These data were collected during a 3-yr study on fall migrants using continuous daily standardized mist-netting from August to October with the same type of nets as in this study (unpubl. data). Habitat distribution differed significantly between calm and windy days (chi-squared test of independence: df = 5, $P < 0.001$). During windy days, proportionally more birds were caught in closed and dense habitats (poplar plantation and within forest) than during calm days. Whether this is a result of higher avoidance rates during windy days or to a different habitat use in response to wind remains an open question.

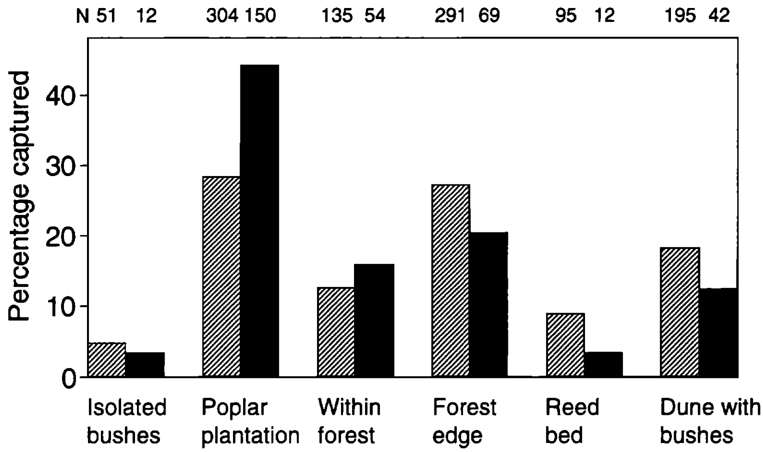

FIGURE 7. Proportion of European Robins caught in different habitats (with various mist net lengths) during calm (Beaufort 0–2; hatched bars) and windy days (Beaufort 3–5; black bars). Numbers above the bars indicate sample sizes.

RECOMMENDATIONS

This study shows that the numbers of birds caught by standardized mist netting can be used to assess habitat use of small bird species (e.g., Bairlein 1981, Berthold 1988, Streif 1991), but with certain reservations.

First, capture numbers from mist netting do not represent quantitatively the composition of species, because capture efficiency strongly varies among species and because the number of birds caught depends on the species-specific spatial and temporal activity patterns (see also Heimerdinger and Leberman 1966, Karr 1981, Pardieck and Waide 1992).

Second, as degree of shading and wind affect capture efficiency, mist nets should be set up in such a way that they are equally exposed to the sun and wind. A straight line of nets in vegetation at least as high as the nets is to be preferred over other net orientations and vegetation heights. It is doubtful that birds flying above the vegetation are adequately represented in the mist net samples. Mist netting operations over many years, however, show that the distribution of a given species over a range of habitats is essentially the same for each year despite variation in weather among years (Berthold 1988).

Third, mist nets should cover the entire vegetation height in order to sample adequately birds preferring the higher vegetation strata. As the highest mist net shelf is more easily avoided, the lower of two superimposed nets probably does not give the same result as a single net. This may also be of importance when investigating vertical distribution patterns.

Fourth, it has to be realized that the numbers of birds caught in mist nets depend on both the density and the activity of the birds. For instance, it has been shown that the diurnal distribution of catching numbers adequately reflects the diurnal activity pattern of individual birds (Brensing 1989, Klein et al. 1971). Hence, a seasonal change in catching frequencies may be the result of a change in activity (e.g., due to molt) and not necessarily to a change in density. An open question is how much the temporal or spatial activity pattern of a given species can vary between habitats at the same time of season.

ACKNOWLEDGMENTS

We thank Gaby Banderet, Teddy Blanc, Romain Cantin and Charly Henninger for letting us use their bird banding site and for their hospitality and help; Thomas Degen, Daniel Friedli, Raffael Winkler and Thomas Weber for their help with the observations, Raffael Winkler for data on skull widths of woodpeckers and F. Bairlein, P. Berthold, B. Bruderer, T. Degen, V. Keller, M. Kestenholz, B. Naef-Daenzer, L. Schifferli, S. E. Wallace, R. Winkler and N. Zbinden for critically commenting on the manuscript.

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Received 6 Apr. 1995; accepted 18 Jul. 1995.