J. Field Ornithol., 68(3):348–357

NET SHYNESS IN THE WOOD THRUSH

BERTRAM G. MURRAY, JR.
Graduate Program in Ecology and Evolution
Rutgers University
Piscataway, New Jersey 08855-1059 USA

Abstract.—Mist-netters have reported a decline in the total number of birds captured (new captures and recaptures) per day over a period of intensive banding and have attributed this decline to "net shyness." If birds were net shy, then mark-recapture estimates of population size from mist-netted samples could be in error. Swinebroad (1964), however, reported that Wood Thrushes (*Hylocichla mustelina*) were recaptured sooner than expected by chance, indicating that they were not net shy. Birds captured sooner than expected by chance, however, also would affect the results of mark-and-release estimates of population size. In exploring the problem further, I mist-netted birds on days separated by at least three days of human inactivity in the area of the nets. There was no tendency for the total number of Wood Thrushes captured to decline from one banding day to the next. Also, Wood Thrushes had a higher probability of being recaptured on the first banding-day after initial capture than they had of being recaptured on a day in the subsequent 3-d-period. I found no reliable evidence for a decline, much less net shyness.

TIMIDEZ DE LAS REDES POR *HYLOCICHLA MUSTELINA*

Sinopsis.—Investigadores que utilizan redes han informado una reducción en el número total de aves capturadas (capturas nuevas y recapturas) por día a través de un período de anillamiento intenso, atribuyendo esta reducción a una "timidez de redes". Si las aves tuvieran "timidez de las redes", los estimados poblacionales por captura-recaptura basados en muestras atrapadas en redes podrían incurrir en errores. Sin embargo, Swinebroad (1964) informó que *Hylocichla mustelina* se recapturaron antes de lo esperado al azar, indicando que no tenían timidez de las redes. Aves capturadas antes de lo esperado también afectarían los resultados de estimados poblacionales basados en captura y liberación. Al explorar este problema, atrapé aves en redes en días separados por la menos tres días de inactividad humana en el area de las redes. No encontré una tendencia de reducción en el número de *Hylocichla mustelina* capturadas entre un día y el siguiente. En adición, las aves tuvieron una major probabilidad de ser recapturadas el primer día después de ser anilladas que de ser atrapadas en cualquier período de '3 días posterior. No encontré ninguna evidencia confiable para reducción en número, mucho menos para tímidez de las redes. Más aąun, no obstante la impresión generalizada entre atrapadores en redes de que hay una reducción en números de capturas en días consecutivos, no hay ninguna publicada.

With the introduction of mist-netting as a means of capturing and marking birds, attempts have been made to estimate the population size of birds with Peterson-type mark-recapture methods (Nichols et al. 1981, Pollock 1981, Stamm et al. 1960, Swinebroad 1964) or regression methods (MacArthur and MacArthur 1974, MacArthur et al. 1972, Terborgh and Faaborg 1973). Mist-netters report that the number of total captures appears to decline over a period of days (Karr 1981, Lovejoy 1975, MacArthur and MacArthur 1974, MacArthur et al. 1972, Stamm et al. 1960). If there is a break in the netting or if nets are moved, the total number of birds caught at first increases, then decreases again. The declines during a period of active netting have been attributed to "net shyness," a change in the catchability of birds. Net shyness could affect the estimated population size (e.g., Nichols et al. 1981). Thus, in estimating numbers from

mist-netted samples, an understanding of so-called net shyness seems necessary.

Net shy birds differ from what have been termed trap-shy birds by bird banders. After the initial capture, a trap-shy bird is rarely caught, even though it may feed in the vicinity of a trap. A trap-happy bird, however, may virtually reside in the trap, some birds returning to the trap as soon as released. Whereas trap-shy and trap-happy are terms referring to the behavior of individual birds following capture, net shyness refers to the effect of netting on the total number of birds actually captured, including those that have not yet been captured. Nevertheless, a few authors have suggested that the decline in number of birds captured is owing to the avoidance of nets *per se* by birds (Karr 1981, Lovejoy 1974, MacArthur and MacArthur 1974, MacArthur et al. 1972).

That birds "avoid" mist-nets seems unlikely. First, the decline in number of total captures per day includes the decline in number of captures of unbanded (i.e., not previously captured) birds. How is it possible for birds that have not been caught in a net to become "net shy"? Second, an analysis of recaptures of mist-netted Wood Thrush (*Hylocichla mustelina*) did not indicate net shyness (Swinebroad 1964). Swinebroad (1964) reported that mist-netted Wood Thrushes had a higher probability of being renetted sooner, rather than later, than expected after initial capture.

In this paper I report the results of an investigation concerned with whether Wood Thrushes tend to avoid mist-nets, using a different method of investigation than that of Swinebroad (1964).

METHODS

In his study of net shyness in the Wood Thrush at Hutcheson Memorial Forest in Somerset County, New Jersey, Swinebroad (1964) used 24 mist nets arranged in a grid pattern, 100 m between nets (see his Figure 1). Because one check of 12 nets required 45 min (if no birds were caught) to more than an hour, each net was checked every 1.0–1.5 h, and only one half the nets could be tended on any day. Swinebroad divided the forest into eastern (E) and western (W) halves.

Swinebroad and his field assistants banded for three, nearly consecutive days, dawn to dusk, in one half and, then, for three, nearly consecutive days in (usually) the other half of the forest (Table 1)—netting during a 3-d period was interrupted only by rain. When not used, the nets were furled in place. Rained-out whole or partial days were made up on the earliest clear day. The first day of banding (7 June), however, was only a half day, and period E4 included only two banding days.

In 1976 I placed my nets at the same net sites and operated dawn to dusk only the E or the W nets on any day (Table 2). In May 1976 I netted alternately between E and W as opportunity allowed (6–10 d between netting in either E or W). In June I netted one day in E, rested one day, netted in W, rested one day, then netted in E. In July I netted every other day in E for three netting days and then every other day in W for three

TABLE 1. Banding days and number of captures in 1962. "N" refers to number of captures of adults for the first time in either area East or West. "R" refers to number of birds captured on a day after initial capture in East or West. "SDR" refers to same-day repeats and may include SDRs of New or Repeat birds. A bird first captured as "New" in East, then recaptured in West, is counted as "New" in West rather than as a "Repeat." Because I have counted the numbers differently, the number of new birds captured and number of repeats on any day do not correspond exactly to the numbers reported by Swinebroad (1964). Note: 7 June was only a half day.

	East					West			
	Captures		SDR			Captures		SDR	
	N	R	No. birds	No. captures		N	R	No. birds	No. captures
E1					W1				
7 June	7	0	0	0	16 June	10	0	1	1
8 June	11	4	2	3	17 June	3	2	0	0
9 June	4	2	0	0	18 June	3	2	1	1
E2					W2				
23 June	11	6	3	3	30 June	11	5	2	2
25 June	6	5	0	0	1 July	6	1	1	1
27 June	8	6	2	2	3 July	2	4	2	2
E3					W3				
28 July	2	2	0	0	14 July	5	2	1	1
29 July	0	5	0	0	15 July	2	4	1	1
31 July	0	2	0	0	19/20 July	0	1	0	0
E4									
4 Aug	0	3	0	0					
5 Aug	1	1	0	0					

netting days. Rained-out whole or partial-days were made up on the next clear day. Thus, there were at least three days without netting activity between netting-days in either E or W in May and June. When I was not netting, the nets were furled in place.

Swinebroad's data naturally fell into 3-d periods (Table 1). To compare the 1976 data with his, I divided the first nine days in E and the first nine days in W into three 3-d periods. After examining my data for May and June (series E1, E2, E3, W1, W2, and W3), which seemed to indicate no net shyness, I became concerned that 1976 was somehow different from earlier years. So, in July I netted a series of three days in east (E4) and then a series of three days in west (W4), netting every other day.

The number of birds captured on any day is a function of the number of birds available in the vicinity of the nets and the probability that each would be caught on any day. The probability of a bird being caught is a function of its species-specific behavior, the position and exposure of the nets, and a host of other factors. To reduce the number of variables, Swinebroad (1964) and I have limited our analyses to a single species and

TABLE 2. Banding days and number of captures in 1976. Definitions for N, R, and SDR as in Table 1.

East					West				
	Captures		SDR			Captures		SDR	
	N	R	No. birds	No. captures		N	R	No. birds	No. captures
E1					W1				
7 May	9	0	2	2	11 May	9	0	2	2
13 May	10	1	0	0	21/22 May	5	4	1	1
23 May	6	0	0	0	27 May	4	1	0	0
E2					W2				
29 May	5	3	0	0	7 June	4	3	1	1
9 June	3	1	1	1	11 June	1	6	2	4
13 June	2	8	1	1	16 June	0	2	0	0
E3					W3				
18 June	2	3	0	0	22 June	2	2	0	0
24 June	5	4	0	0	27 June	3	3	0	0
30 June	6	7	0	0	2 July	0	3	0	0
E4					W4				
6 July	2	5	0	0	15 July	1	3	0	0
8 July	2	5	0	0	18 July	2	0	0	0
10 July	1	0	0	0	20 July	0	2	0	0

placed the nets in a fixed grid pattern covering the entire woodlot. No bird could be more than 71 m from a net. We cannot calculate the probability of a bird being captured without knowing the number of birds present, but we can measure the probability of already captured birds being recaptured (Swinebroad 1964). Net shyness implies that the probability of a bird being captured on day 2 is lower than that for being captured on day 1 and that the probability of being captured after a break in netting activity should be greater than the probability of being recaptured on day 2 (Stamm et al. 1960). Because it is impossible to calculate the probability of capture for a population of unknown size, I have focussed attention on the probabilities of being recaptured (Swinebroad [1964] estimated the probability of capture in 1962 by considering only the birds caught in 1962 that returned in 1963). If net shyness among birds is a reality, we should expect that the probability of being recaptured shortly after capture is lower than the probability of being recaptured after a longer break in netting activity in an area.

In analyzing his data, Swinebroad (1964) used the method of Young et al. (1953) for calculating the probability of a bird being first recaptured on the *n*th day after initial capture. He showed that captured Wood Thrushes were recaptured shortly after initial capture more frequently than expected by chance, indicating that they were not net shy.

I approached the problem of net shyness differently and, I think, more

Banding Period 1			Banding Period 2			Banding Period 3			Banding Period 4		
Day 1	Day 2	Day 3	Day 1	Day 2	Day 3	Day 1	Day 2	Day 3	Day 1	Day 2	Day 3
$N_{i(1)}$	$N_{i(2)}$ + $R_{i(1)}$	$N_{i(3)}$ + $R_{i(2)}$	R_s	R_s	R_s	R_s	R_s	R_s	R_s	R_s	R_s
			$N_{i(1)}$	$N_{i(2)}$ + $R_{i(1)}$	$N_{i(3)}$ + $R_{i(2)}$	R_s	R_s	R_s	R_s	R_s	R_s
						$N_{i(1)}$	$N_{i(2)}$ + $R_{i(1)}$	$N_{i(3)}$ + $R_{i(2)}$	R_s	R_s	R_s
									$N_{i(1)}$	$N_{i(2)}$ + $R_{i(1)}$	$N_{i(3)}$ + $R_{i(2)}$

FIGURE 1. Banding protocol and calculation of probabilities. There are four 3-day banding periods in each sector of the forest, E and W. In the first banding period, only new birds and repeats of new birds may be captured. In the second, third, and fourth banding periods, new birds, repeats of new birds, and repeats from previous banding periods may be captured. Thus, second, third, and fourth banding periods can be the initial period for some birds (newly caught) and subsequent period for other birds (repeats). In this figure, $N_{i(1)}$, $N_{i(2)}$, and $N_{i(3)}$ represent the numbers of birds captured for the first time on days 1, 2, and 3, respectively, of the initial period, $R_{i(1)}$ and $R_{i(2)}$ are the number of repeats from the preceding day of the initial period, and R_s is the number of birds captured from previous banding periods. What have not been counted are same-day-repeats, captures of birds on day 3 also captured on day 1 and day 2 of an initial banding period, and repeats of repeaters within a subsequent banding period (see Table 4). Birds recaptured in second and third subsequent periods (the shaded portion) do not enter into the calculation of P_i and P_s. The data, however, are presented in Table 3.

P_i is determined by summing $R_{i(1)}$ and $R_{i(2)}$ from the initial banding period and dividing by the sum of $N_{i(1)}$ and $N_{i(2)}$ from the initial banding period (see Eq. 1). P_s is determined by summing R_s from all days of the subsequent banding period and dividing by the sum of $N_{i(1)}$, $N_{i(2)}$, and $N_{i(3)}$ from the preceding initial banding period (see Eq. 2).

simply. For this analysis, I distinguish between "initial" and "subsequent" 3-d periods (Figure 1; Table 3). The initial 3-d period is the one in which a particular bird is first captured. Subsequent 3-d periods are those following the initial period for a particular bird. A 3-d period, then, may be the initial period for some birds (newly captured) and subsequent for others (first captured in an earlier 3-d period). Given this distinction, I compared the proportion of birds recaptured on the first-banding day after their initial capture (within the initial 3-day period) with the proportion recaptured per day in the *immediately following* 3-d period.

The proportion of birds that were recaptured on the first banding day following their initial capture (within the initial 3-day period) is given by,

$$P_i = \frac{\text{number of birds recaptured on the first banding day after initial capture}}{\text{number of birds first caught on day 1 or day 2 of initial 3-d period}}. \quad (1)$$

TABLE 3. A comparison of the proportion of Wood Thrushes recaptured on the day after initial capture with the proportions recaptured on later days. In the initial period, N_i is the number of birds newly caught on day 1 or day 2 (birds caught on day 3 are not counted because they cannot be recaught in initial period), R_i is the number recaptured on the day after original capture, and P_i is the proportion recaptured on the day after original capture. In subsequent 3-day periods, N_s is the number of birds captured on all 3 days of the initial 3-day period, R_s is the number recaptured, and P_s is the proportion that was recaptured per day.

				Subsequent 3-day period								
	Initial period			First			Second			Third		
Sample	N_i	R_i	P_i	N_s	R_s	P_s	N_s	R_s	P_s	N_s	R_s	P_s
62E-1	18	5	0.278	22	12	0.182	22	5	0.076	22	2	0.030
62E-2	19	1	0.053	27	2	0.025	27	1	0.012			
62E-3	2	0	0.000	2	1	0.167						
Total	39	6	0.154	51	15	0.098	49	6	0.041	22	2	0.030
62W-1	13	2	0.154	16	6	0.125	16	2	0.042			
62W-2	17	1	0.059	19	4	0.070						
Total	30	3	0.100	35	10	0.095	16	2	0.042			
76E-1	19	1	0.053	25	8	0.107	25	8	0.107	25	4	0.053
76E-2	8	2	0.250	10	2	0.067	10	4	0.133			
76E-3	7	1	0.143	13	1	0.026						
Total	34	4	0.118	48	11	0.076	35	12	0.114	25	4	0.053
76W-1	14	5	0.357	18	9	0.167	18	3	0.056	18	2	0.037
76W-2	5	1	0.200	5	1	0.067	5	1	0.067			
76W-3	5	0	0.000	5	2	0.133						
Total	24	6	0.250	28	12	0.143	23	4	0.058	18	2	0.037

There is no "day after" for birds caught on day 3 of a 3-d period. Thus, only birds caught on day 1 or day 2 could be recaptured on a "day after" and be counted in the denominator.

The proportion of birds recaptured *per day* during subsequent 3-d periods is given by,

$$P_s = \frac{\text{number of birds recaptured in the subseqent 3-d period}}{\text{number of birds captured in initial 3-d period}} \div 3$$

that is,

$$P_s = \frac{\text{number of birds recaptured in the subsequent 3-d period}}{\text{number of birds captured in initial 3-d period} \times 3}. \quad (2)$$

Both the numerator and denominator include the birds first caught on day 3 of the initial period. Thus, the sample size (given in Table 3) for subsequent 3-d periods is larger than that for birds first captured in the initial period.

I included data on the probability of recapture for subsequent periods 2 and 3 in Table 3, but these are not used in the comparison because the sample size inevitably becomes smaller and the sample is farther from the period of initial capture.

TABLE 4. Birds caught on three consecutive days of initial period, birds caught on two consecutive days in subsequent periods, and same-day-repeats of Wood Thrushes in 1962 and 1976 at HMF.

Sample	Birds caught on 3 consecutive days of initial period	Birds caught on 2 consecutive days in subsequent periods	Same-day repeats	
			No. birds	No. repeats
1962				
E1	1	—	2	3
E2	0	1	5	5
E3	0	1	0	—
W1	0	—	2	2
W2	1	0	5	5
W3	0	1	2	2
1976				
E1	0	—	2	2
E2	0	0	2	2
E3	0	3[a]	0	0
E4	0	1	0	0
W1	0	—	3	3
W2	0	1	3	5
W3	0	2	0	0
W4	0	0	0	0

[a] Includes one bird caught on three consecutive days.

In both 1962 and 1976 birds were released at the site of capture.

RESULTS

Total captures.—In 1962 at Hutcheson Memorial Forest the number of captures of Wood Thrushes tended to decline when nets were used on consecutive days or nearly consecutive days (Table 1). Of the six instances (E2, E3, E4, W1, W2, W3) from day 1 to day 2 of a 3-d period, five showed a decline, one an increase (note that E1 is not included because "day 1" was only a half-day and that E4 is included even though it is a 2-d period). Of the six instances from day 2 to day 3 (E1, E2, E3, W1, W2, W3), four showed a decline, one no difference, and one an increase. Thus, a decrease in captures occurred in 9 of 12 pairs of days.

In 1976, when several days of inactivity separated banding days, the pattern appeared to be different (Table 2). Of six instances (E1, E2, E3, W1, W2, W3) from day 1 to day 2, three showed an increase, one a decrease, and two no difference. Of the six instances from day 2 to day 3, two showed an increase, and four showed a decrease. Thus, a decrease occurred in only 5 of 12 pairs of days.

When I netted on alternate days within an area in 1976 (E4 and W4), there were two decreases, two no difference, and no increases (Table 2). The samples were small, but they contribute to the impression of a decline in captures when netting days are close.

Although the tendency toward decline on successive days of banding is apparent, the sample is too small to provide statistically significant results. Unfortunately, most promoters of the notion of net shyness have not published data on the decrease, and no one has published a statistically significant demonstration of a decline in captures on successive days of netting. Thus, the decline in numbers on consecutive days of netting may be more apparent than real.

Recaptures.—In both East and West and in both 1962 and 1976 the tendency was for the proportion of birds recaptured on the first banding day after initial capture to be greater than the proportion recaptured per day in the subsequent 3-d period (Table 3).

The proportion of birds recaptured on the day after being captured for the first time is an underestimate of the probability of being recaptured shortly after being captured because I have not included in this analysis (i) birds caught on the third day of an initial 3-d period if it had been caught on both day 1 and day 2, (ii) birds caught on two consecutive days in a subsequent 3-d period, and (iii) same-day-repeats (Table 4).

There is, then, no indication of net shyness or net avoidance by captured birds, either in 1962, when a decline in total number of birds captured was apparent, or in 1976, when a decline was not evident. Wood Thrushes have a higher probability of being captured on the day after first being captured than at a later time.

Discussion

The impression that the number of birds caught in mist nets declines over a period of days is sufficiently strong that it has been explained to be the result of "net shyness" or "net avoidance" (Karr 1981, Lovejoy 1974, MacArthur and MacArthur 1974, MacArthur et al. 1972, Stamm et al. 1960, Swinebroad 1964). The 1962 data (when nets were used on nearly consecutive days) are certainly suggestive (9 of 12 pairs of days showing declines in number of birds captured from one day to the next), but the sample size is small (Table 1). The 1976 data (when netting was done every fourth day) are not (7 of 16 pairs of days showing declines; Table 2).

A problem for the net shyness interpretation is that newly captured birds (if the Wood Thrush is typical) have a higher probability of being recaptured sooner rather than later after initial banding (Table 3; Swinebroad 1964). If the decline in total numbers captured (new captures plus recaptures) is real, then one must wonder why birds not yet captured avoid the nets while already captured birds do not. I suggest that birds may not be avoiding nets per se, but rather they are avoiding areas of human activity.

A reviewer of this manuscript suggested that birds often hit nets and escape, as reported by Jenni et al. (1996) and observed by many others, which may account for unbanded birds becoming net shy. This solution fails to account for the greater probability of being recaptured of birds caught and banded. If birds that are captured and handled have a higher

probability of being recaptured on the next netting day than on a later day, as indicated by my results and those of Swinebroad (1964) on the Wood Thrush, I suggest that birds are not net shy and that net shyness is not the cause of a decrease in the decline in number of birds caught on consecutive days of netting.

An alternative is the possibility that birds avoid areas of human activity at the netting site, as suggested by Lovejoy (1974). He called this "net avoidance," which is a misleading characterization if birds are in fact avoiding humans rather than the nets. Birds could avoid areas of human activity with no knowledge of the location or even existence of the nets. Furthermore, we are still left with accounting for two populations of birds—banded birds that are more likely to be recaught the following day, apparently lacking net shyness caused by previous capture and handling, and unbanded birds (whether they escape from a net or not) that for some reason avoid the nets and cause the apparent decline in total captures from one day to the next. Until we have a better grasp of the effect that netting activity has on the probabilities of capturing birds and of recapturing them, perhaps we should avoid using mark-recapture methods in estimating population size.

Nevertheless, because there does seem to be a decline, even if small, in new captures when netting activity occurs on consecutive or nearly consecutive days but not when netting is interrupted by 3-d rest, perhaps one should not net on consecutive days or even every other day in an area.

ACKNOWLEDGMENTS

I thank Jeff Swinebroad for allowing me access to his 1962 records and to him, E. H. Burtt, Jr., J. Faaborg, and two anonymous reviewers for their comments on the manuscript, Robert E. Loveland for statistical advice, and the Frank M. Chapman Memorial Fund of the American Museum of Natural History for funds to buy net poles without which this project could not have been undertaken.

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Received 18 Mar. 1996; accepted 26 Aug 1996.

UPCOMING MEEETINGS

Association of Field Ornithologists.—75th anniversary meeting jointly with the American Birding Association, 21–26 Jul. 1997, San Jose, Costa Rica. Registrar: Carol Wallace, American Birding Association, P.O. Box 6599, Colorado Springs, Colorado 80934-6599 (800-850-2473).

Society of Caribbean Ornithology.—1–6 Aug. 1997, Aruba, Dutch West Indies. For information contact Joseph M. Wunderle, President, SCO, P.O. Box 507, Palmer, Puerto Rico 00721.

American Ornithologists' Union.—115th stated meeting, 13–16 Aug. 1997, University of Minnesota, Minneapolis, Minnesota. For information contact Francesca Cuthbert (cuthb@maroon.tc.umn.edu) or Peter Lowther (lowther@fmnh.org).

Western Field Ornithologists.—21–24 Aug. 1997, Imperial Valley, California. For information contact Kimball L. Garrett (Natural History Museum of Los Angeles County, 900 Exposition Blvd., Los Angeles, California 90007) or Philip Unitt (San Diego Natural History Museum, P.O. Box 1390, San Diego, California 92112).

Western Bird Banding Association.—2–4 Oct. 1997, Ash Meadows National Wildlife Refuge, Pahrump, Nevada. For information contact Ken Voget, 1500 N. Decatur Blvd., Las Vegas, Nevada (702-646-3401).