Florida (Wood and Collopy 1993). The relatively consistent interval between loss of a first clutch and initiation of a second in raptors is likely controlled by changes in hormone levels (e.g., prolactin) that cause ovulation to cease after incubation begins (Welty 1982). After an initial clutch is lost, it apparently takes a minimum of 1–3 weeks for hormone levels to change enough to stimulate ovulation of a second clutch.

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LITERATURE CITED

BENT, A. C. 1938. Life histories of North American birds of prey. Part 2. Smithsonian Institution U.S. Natl. Mus. Bull 170.

BULL, E. L., AND M. G. HENJUM. 1990. Ecology of the Great Gray Owl. USDA For. Serv. Gen. Tech. Rept. PNW-GTR-265.

CADE, T. J., AND S. A. TEMPLE. 1977. The Cornell University falcon programme, p. 353–369. *In* Proc. International Council For Bird Preservation, World Conf. on Birds of Prey, Vienna.

FORSMAN, E. D. 1981. Molt of the Spotted Owl. Auk 98:735–742.

FORSMAN, E. D., E. C. MESLOW, AND H. M. WIGHT. 1984. Distribution and biology of the Spotted Owl in Oregon. Wildl. Monogr. 87.

FRY, C. H., S. KEITH, AND E. K. URBAN. 1988. The birds of Africa, Vol. III. Academic Press, London.

KROEL, K. W., AND P. J. ZWANK. 1992. Renesting of Mexican Spotted Owl in southern New Mexico. J. Raptor Res. 26:267–268.

LEWIS, J. C., AND B. C. WALES. 1993. Northern Spotted Owl pair successfully renests. J. Field Ornithol. 64:323–325.

NEWTON, I. 1979. Population ecology of raptors. Buteo Books, Vermillion, SD.

PLATT, J. B. 1977. The breeding behavior of wild and captive Gyr Falcons in relation to their environment and human disturbance. Ph.D.diss., Cornell Univ., Ithaca, NY.

SCLATER, W. L. 1912. A history of the birds of Colorado. Witherby, London.

SOUTHERN, H. N. 1970. The natural control of a population of Tawny Owls (*Strix aluco*). J. Zool. London 62:197–285.

WELTY, J. C. 1982. The life of birds. Saunders College Publishing, New York.

WOLFE, R. 1912. The Western Horned Owl in western Kansas. Oologist 29:222–224.

WOOD, P. B., AND M. W. COLLOPY. 1993. Effects of egg removal on Bald Eagle productivity in northern Florida. J. Wildl. Manage. 57:1–9.

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REPERTOIRES, TERRITORY SIZE AND MATE ATTRACTION IN WESTERN MEADOWLARKS[1]

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Key words: Western Meadowlarks; Sturnella neglecta; *repertoires; signature songs; territories; mating status.*

Male Western Meadowlarks (*Sturnella neglecta*) are conspicuous in their singing activity as they establish and defend their chosen territories (Lanyon 1957). Meadowlark females arrive only after the males have begun this process of defense (Lanyon 1956). The song delivery of a male Western Meadowlark consists of a repertoire of discreet, stereotypical song types, each of which is repeated several times before switching to another (Miller 1952, Falls and Krebs 1975). Each male sings between three and 12 song types, about one third of which are shared by neighboring birds (Horn 1987). The individual song types do not carry different messages (Horn and Falls 1988), nor are they associated with specific behaviors (Horn and Falls 1991). However, the action of switching song types within a repertoire in itself apparently conveys a message that the territory is being actively defended (Falls and d'Agincourt 1982). This is evidenced by the fact that switching is more rapid during boundary defense activity than before or afterward (Horn and Falls 1991).

Several investigators have tested the association between song delivery and territory control in a variety of avian species. Yasukawa (1981) showed that Red-winged Blackbird (*Agelaius phoeniceus*) repertoires conferred an advantage over single song-types in territory defense. Krebs et al. (1978) suggested that in the Great Tit (*Parus major*) large repertoires were more effective than small ones in keeping out intruding males. Correlations between repertoire size and territory size have been found to exist in several species, including the Great Tit (Krebs 1977b), the Northern Mockingbird (*Mimus polyglottos*; Howard 1974), and the Red-winged Blackbird (Yasukawa et al. 1980). Female use of repertoire clues has also been investigated. Catch-

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pole (1980) noted that male Sedge Warblers (*Acrocephalus schoenobaenus*) with large syllable repertoires attracted females earlier than ones with small repertoires, and Howard (1974) found the same to be true for mockingbirds. Horn et al. (1993) observed a significant correlation between repertoire size and reproductive success in Western Meadowlarks.

A number of theories have been proposed that could account for the effectiveness of large repertoires in territory defense. (1) Falls and d'Agincourt (1982) suggest rapid switching among songs in a repertoire may signal to intruders a readiness to take action. The effect of this tactic would be enhanced with larger repertoires since the bird would have more songs to choose from in his effort to keep his delivery varied and unpredictable and therefore less subject to habituation by his listener. (2) An interloper may avoid an area occupied by a large repertoire singer, considering it crowded, as suggested by Krebs (1976, 1977a) and thus leave a larger area for the resident. (3) Western Meadowlarks show a tendency to respond to potential intruders by matching their song types (Falls 1985). A large repertoire could provide the singer with more opportunity for such matching and the intruding rivals would thereby be induced to retreat (Krebs et al. 1978). (4) Conversely, large repertoires are more difficult for intruding birds to learn and therefore match, when attempting to displace a current resident (Craig and Jenkins 1982).

Could any of these hypotheses have a bearing on female behavior? The arriving female has her own set of goals, such as being able to assess territory attributes and/or male quality (Searcy and Andersson 1986). Fundamental to this is the ability to recognize the male. However if large repertoires are more difficult to learn, as Craig and Jenkins (1982) suggest, then male recognition by females in search of a mate and a territory would be hampered rather than enhanced by large repertoires. Perhaps there is an aspect of large repertoires which contributes to making them more recognizable. They might have a greater likelihood of including unique songs, unshared by neighboring males. Could the presence or the number of such songs in a repertoire affect male success in attracting a mate? Weary et al. (1990) refer to these songs as signature songs and suggest that for Great Tits, at least, they may be one of several cues by which birds recognize individuals.

The purpose of this study was to determine the relationships among repertoire characteristics, territory size and mate attraction in Western Meadowlarks. It is generally agreed that bird song functions to proclaime a territory and attract a mate (Krebs et al. 1978). If this is the case, one might expect to find an association between repertoire characteristics and territory sizes among male Western Meadowlarks. One might hypothesize that mating success would also be associated with these characteristics.

METHODS

This investigation was conducted in a 16 ha meadow southeast of Boulder, Colorado during the years 1986–1994. Males were identified by their repertoires, which remain constant throughout a season (Falls 1985) and which rarely change even over multiple years (Horn 1987). Repertoire sizes in this study ranged from four to nine song types. In all, 33 male bird-years were observed. This included birds which returned for multiple seasons and were recognized by ear from their repertoires, upon their return. Returning males from previous seasons were considered anew every year when counting the number of birds present. Returning birds were also included for the purpose of identifying signature songs, since the definition of a given song as a signature song depends upon whether or not it is shared by neighboring birds. These returning birds, however, were not included in data analysis.

Each year the song repertoires of all males settling in the study area were recorded and their territories measured. Female response to male activity was observed and recorded. Females made their arrival and subsequent residency on a territory apparent by their characteristic trill, which is added to the last syllable of the song-type repeats of her mate. Territory sizes did not change when a male acquired a female. Most Western Meadowlark males are bigamous (Lanyon 1956), usually pairing sequentially (Dickinson and Falls 1989). Since the secondary female rarely interacts with the male (Horn 1987), I examined the first females' activities only. I was unable to determine if any of these birds returned for multiple years.

Songs and trills were recorded using a Sony TCM-500 EV cassette recorder, with built-in directional microphone. Birds were observed while being recorded and care was taken not to walk or place equipment on the territories while recording. All recordings were of a quality which permitted sonograms to be made (Kay Elemetrics 6061B Sona-graph with wide-band setting), from which the differences between song types in a bird's repertoire were clearly discernible. The songs of Western Meadowlarks are easily distinguishable by ear and sonograms confirmed aural classifications.

A territory was defined as the area which included all the perches from which a given male sang. This was also the area from which other singing conspecific males were excluded. The size of each bird's territory was determined by plotting its singing perches (Simpson 1984) on an aerial-photography map produced by the Boulder (Colorado) County Land Use Department (1: 200 scale). The outermost perches were joined by lines to form a minimum convex polygon (Odum and Kuenzler 1955, Picman 1987) and the area of the polygon was calculated in square meters. The associations among territory sizes, repertoire sizes and eventual mating status were analyzed statistically.

The repertoires for all males in each season were compared and the number of shared and unshared song types for each bird were noted. Signature songs were defined as those not shared by any other singers in the study area. No effort was made to track song sharing with birds outside of the study area. The same correlations were computed for the number of signature songs in a repertoire as for the absolute repertoire sizes.

Birds were observed almost daily throughout the breeding season (mid-March through mid-June) and their perches were noted and songs recorded at random times throughout each day.

RESULTS

The number of males sharing the study area each year ranged from two to six and the number of signature

TABLE 1. Correlation between variables associated with repertoire size, for 24 males.

	Repertoire size	Number of signature songs	Territory size
Repertoire size	—	0.275	0.395
Number of signature songs	0.022	—	0.348
Territory size	0.003	0.009	—

Kendall's τ, corrected for ties, is above the diagonal; P values are below diagonal.

songs per bird ranged from zero to five. In those years when fewer males shared the area, individuals held larger territories (Kendall's $\tau = -0.243$, $P = 0.047$, $n = 33$) and included more signature songs within their repertoires ($\tau = -0.389$, $P = 0.001$, $n = 33$) than did birds settling in years with higher populations. These two correlations in themselves would result in a strong association between signature songs and territory size, obscuring relationships between either one of these variables and the other factors studied. Omitting years when only two males occupied the study area resulted in a weaker relationship between the number of birds sharing the locale and both territory size ($\tau = -0.542$, $P = 0.4715$) and number of signature songs ($\tau = -0.161$, $P = 0.238$). Therefore, to avoid confounding associations with numbers of residents, these two-male years were omitted from all subsequent correlations. (There were three such years; $n = 27$ male-years remaining, including returning birds; $n = 24$ males, excluding returns.)

There was a significant positive association between territory and repertoire sizes and also between territory size and the number of signature songs in the repertoire. The correlation between the number of signature songs and the total number of songs in the repertoire was positive (Table 1).

Mated males averaged more signature songs in their repertoires than unmated ones. The average total repertoire size of mated males was significantly larger than that of unmated ones. Mated males held considerably larger territories than did unmated males which was reflected in a slight, but not significant, negative association between mating success and male population density (Table 2).

DISCUSSION

The observations reported here demonstrate a positive correlation between repertoire characteristics (size and uniqueness) and territory sizes in Western Meadowlarks. Both a large territory and a large and distinctive repertoire appeared to confer an advantage upon a male in his success in finding a mate. Sample sizes in this study were inadequate to permit partial correlations, which might have demonstrated the independent effects of these variables.

Since male Western Meadowlarks arrive and settle onto their territories before the appearance of the females, a system should be favored whereby the female, when she arrives, would be able to evaluate a territory. Finding a large domain is especially valuable for the female in a polygynous species such as the Western Meadowlark since she assumes the greater share of feeding the young (Lanyon 1957). In addition, it is highly probable that a given meadowlark female eventually will have to share the territory with another female (Dickinson et al. 1987). Territory size cannot be determined without boundary awareness and boundary awareness is facilitated by recognition of the defending male. Only after the female is aware of the boundaries, can she make an assessment of what is inside them. Repertoire characteristics could be signals by which she could determine the boundaries of a prospective territory. That a male's singing activity diminishes after he has attracted a female (Horn and Falls 1991) supports this concept.

These results suggest that repertoire characteristics may help a female define territories. Conclusions about the effects of signature songs, however, must be made with caution, since repertoires adjacent to, but outside of the study area, were not recorded and therefore the number of signature songs for each bird was almost certainly overestimated. No matter how far a study area were extended, there would still be outside neighbors and signature songs would still be overrepresented. Also, the slight (but insignificant) positive relationship between mating success and lower population density, might be an influential factor in the association between signature songs and mating success (Table 2). With these qualifications in mind, one can nevertheless speculate on the role of this association in the reproductive success of Western Meadowlarks. The number of signature songs included could be an effective feature of repertoire size for female recognition of the owner of a territory. Unique songs are the salient method whereby humans most quickly recognize individual birds. Could this be true also for female meadowlarks? Horn (1987) and others (Falls et al. 1988) observed that male Western Meadowlarks, when matching songs, classified the same sets of song types as being similar, as human listeners did. Further study with a larger sample size could show to what extent the number of

TABLE 2. Mean song and territory attributes of mated and unmated males.

	Mated ($n = 17$)	Unmated ($n = 7$)	Mann-Whitney U	P
Average number of songs in repertoire	6.294	5.000	29.0	0.046
Average number of signature songs	2.529	1.143	30.0	0.055 (ns)
Average territory size	12,406.824 m^2	3,228.143 m^2	10.0	0.002
Average number of males sharing study area per year	5.000	5.714	39.5	0.134 (ns)

unique song types is a feature of repertoire size which is of significance in attracting a mate and could suggest a reason for the correlation between territory size and total repertoire size.

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LITERATURE CITED

CATCHPOLE, C. K. 1980. Sexual selection and the evolution of complex song among European Warblers of the genus *Acrocephalus*. Behaviour 74: 149–166.

CRAIG, J. L., AND P. F. JENKINS. 1982. The evolution of complexity in broadcast song of passerines. J. Theor. Biol. 95:415–422.

DICKINSON, T. E., AND J. B. FALLS. 1989. How Western Meadowlarks respond to simulated intrusions by unmated females. Behav. Ecol. Sociobiol. 25: 217–225.

DICKINSON, T. E., J. B. FALLS, AND J. KOPACHENA. 1987. Effects of female pairing status and timing of breeding on nesting productivity in Western Meadowlarks (*Sturnella neglecta*). Can. J. Zool. 60:3093–3101.

FALLS, J. B. 1985. Song matching in Western Meadowlarks. Can. J. Zool. 63:2520–2524.

FALLS, J. B., AND J. R. KREBS. 1975. Sequence of songs in Western Meadowlarks (*Sturnella neglecta*). Can. J. Zool. 53:1165–1178.

FALLS, J. B., AND L. G. D'AGINCOURT. 1982. Why do meadowlarks switch song types? Can. J. Zool. 60:3400–3408.

FALLS, J. B., A. G. HORN, AND T. E. DICKINSON. 1988. How Western Meadowlarks classify their songs; evidence from song matching. Anim. Behav. 36: 579–585.

HORN, A. G. 1987. Repertoires and song switching in Western Meadowlarks (*Sturnella neglecta*). Ph.D. diss., Univ. of Toronto, Toronto, Ontario.

HORN, A., AND J. B. FALLS. 1988. Structure of Western Meadowlark (*Sturnella neglecta*) song repertoires. Can. J. Zool. 66:284–288.

HORN, A., AND J. B. FALLS. 1991. Song switching in mate attraction and territory defense by Western Meadowlarks (*Sturnella neglecta*). Ethology 87: 262–268.

HORN, A. G., T. E. DICKINSON, AND J. B. FALLS. 1993. Male quality and song repertoires in Western Meadowlarks (*Sturnella neglecta*). Can. J. Zool. 71:1059–1061.

HOWARD, R. D. 1974. The influence of sexual selection and interspecific competition on mockingbird song (*Mimus polyglottos*). Evolution 28:428–438.

KREBS, J. R. 1976. Bird song and territorial defense. New Scientist 70:534–536.

KREBS, J. R. 1977a. The significance of song repertoires: the Beau Geste hypothesis. Anim. Behav. 25:475–478.

KREBS, J. R. 1977b. Song and territory in the Great Tit (*Parus major*), p. 44–62. *In* B. Stonehouse and C. M. Perrins [eds.], Evolutionary Ecology Mcmillan, London.

KREBS, J., R. ASHCROFT, AND M. WEBBER. 1978. Song repertoires and territory defense in the Great Tit. Nature 271:539–542.

LANYON, W. E. 1956. Territory in the meadowlarks, genus *Sturnella*. Ibis 98:485–489.

LANYON, W. E. 1957. The comparative biology of the meadowlarks (*Sturnella*) in Wisconsin. Publ. of the Nuttall Ornithol. Club. 1:1–67.

MILLER, L. 1952. Songs of the Western Meadowlark. Wilson Bull. 64:106–107.

ODUM, E. P., AND E. KUENZLER. 1955. Measurement of territory and home range size in birds. Auk 72: 128–137.

PICMAN, J. 1987. Territory establishment, size and tenacity by male Red-winged Blackbirds. Auk 104: 405–412.

SEARCY, W. A., AND A. ANDERSSON. 1986. Sexual selection and the evolution of song. Ann. Rev. Ecol. Sys. 17:507–533.

SIMPSON, B. S. 1984. Tests of habituation to song repertoires by Carolina Wrens. Auk 101:244–254.

WEARY, D. M., K. J. NORRIS, AND J. B. FALLS. 1990. Song features birds use to identify individuals. Auk 107:623–625.

YASUKAWA, K. 1981. Song repertoires in the Red-winged Blackbird (*Agelaius phoeniceus*): a test of the Beau Geste hypothesis. Anim. Behav. 29:114–125.

YASUKAWA, K., J. L. BLANK, AND C. B. PATTERSON. 1980. Song repertoires and sexual selection in the Red-winged Blackbird. Behav. Ecol. Sociobiol. 7:233–238.