FACTORS AFFECTING ESTIMATES OF CALIFORNIA GNATCATCHER TERRITORY SIZE

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Efforts to conserve the California Gnatcatcher (*Polioptila californica*) have generally focused on maintaining large, viable tracts of coastal sage scrub habitat through regional land-use planning, rather than on delineation and protection of specific areas used by individual pairs (Atwood and Noss 1994, Reid and Murphy 1995). Nonetheless, determination of the territory or home-range boundaries of particular pairs of gnatcatchers is sometimes an issue of management and regulatory concern. For instance, property owners who prepare habitat-conservation plans under Section 10(a) of the Endangered Species Act usually base mitigation proposals on the level of gnatcatcher "take" expected to result from the proposed project (Bean et al. 1991). Because this species inhabits some of the most expensive real estate in the United States, determining the number of pairs likely to be affected by a proposed development—and the amount of mitigation that may be required—can easily have major financial implications. Furthermore, estimates of gnatcatcher territory or home-range sizes have been suggested as possible indices of habitat quality (Atwood 1993). Because population-viability models frequently determine carrying capacity from classification of habitat quality (Akçakaya and Atwood 1997), the comparability of territory-size estimates obtained by different researchers using various techniques is an important issue that may influence regional conservation planning.

Published information concerning the home-range or territory sizes of California Gnatcatchers is limited (Atwood 1993), and statements made in various unpublished reports and planning documents have in some cases been cited so frequently that the preliminary nature of the original comments seems often to have been forgotten. It is not the intent of this paper to critique the results of other studies or even to summarize information on territory sizes presented to date. Instead, our focus here is to use data from the Palos Verdes Peninsula to assess factors that may influence the analysis of gnatcatcher home-range or territory sizes and to propose some general approaches to this topic that would enhance our ability to synthesize information being generated by various ongoing studies.

METHODS

During 1993 and 1994 we mapped the use areas (here we make no effort to distinguish the terms use area, home range, or territory) of 26 breeding pairs of the California Gnatcatcher on the Palos Verdes Peninsula, Los Angeles County, California. Observations were recorded on 7.5-minute-series USGS topographic maps enlarged to a scale of approximately 1 inch = 500 feet. Although vocal and visual registrations of both sexes were used, the majority of our data reflect locations of the more easily observed males. If both birds of a pair were recorded simultaneously, only the male's position was used in the analysis. When a pair rotated nest-attending duties during an observation, the bird that earlier had been attending the nest became the focal individual for the duration of the observation. Although locations of fledglings were mapped similarly, they were not included in the following analyses.

Playbacks of tape-recorded vocalizations or "spishing" were only rarely used to relocate birds that had temporarily disappeared from view. Observations were generally made from distances greater than 50 m to reduce the possibility that normal behavior might be influenced by the researcher. Thirteen (50%) of the observed pairs included at least one uniquely color-banded bird. Behavioral details and information concerning reproductive status were recorded during each visit, as well as during supplemental visits when specific locations were not mapped.

Pairs were visited on varying numbers of dates from late February through early August, with most observations being made during the mid-morning hours (Table 1). On each date we attempted to obtain at least 10 observations spaced at 5-minute intervals; points recorded at shorter intervals were excluded. In reality, gaps between successive observations were often longer than 5 minutes, and on some days it proved impossible to obtain the desired 10 data points given our project's time constraints.

As an initial step toward reducing potential bias, thought to be especially likely when a pair's secretive behavior on a given date might force an observer to establish visual contact by waiting for the birds' appearance near a previously identified nest, prior to analysis we restricted the data as follows. First, dates represented by fewer than five points were excluded. Second, observation periods were not allowed to include gaps longer than 60 minutes; points isolated by such gaps were excluded. Third, on dates when locations were mapped during morning and afternoon hours, and where both visits met the preceding criteria, the afternoon records were excluded. Finally, after imposing these limitations, we restricted the sample size again, removing dates represented by fewer than five points. The resulting data are summarized in Table 1.

We entered the locations in a computer and converted them to UTM coordinates by using the ArcInfo geographic-information system. Analysis was performed by means of the CALHOME home-range-analysis program developed by the U.S. Forest Service and California Department of Fish and Game (Kie et al. 1994, Larkin and Halkin 1994). As provided by CALHOME, we applied the adaptive-kernel method of Worton (1989), the harmonic-mean method of Dixon and Chapman (1980), and the minimum-convex-polygon method of Mohr (1947) to various data subsets described below. Except when evaluating the effects of different grid densities (see below), we used a 25-m grid-cell size for both adaptive-kernel and harmonic-mean analyses. For both of these nonparametric methods of estimating use area we calculated the 75% and 90% point-distribution contours, constructing the minimum convex polygon containing 100% of the observation points.

We tested the assumption that successive data points were independent by using observations from 20 randomly selected dates, representing 14 different pairs of gnatcatchers. Following the approach outlined by Swihart and Slade (1985), we calculated Schoener's ratio for observations obtained

Table 1 Data Used in Analyses of California Gnatcatcher Use Areas

Pair	Days studied[a]	Date range	Modal time of visits	Number of nests[b]
93G01	15	10 Mar-24 Jun 1993	07:30	(1)
93G02	25	9 Mar-1 Jul 1993	08:30	2
93G03	23	9 Mar-2 Jul 1993	10:45	3
93G04	38	9 Mar-3 Jul 1993	06:45	(2)
93G05	29	9 Mar-4 Aug 1993	09:50	3
93G06	26	9 Mar-13 Jul 1993	09:10	(2)
93G07	28	10 Mar-3 Aug 1993	09:25	3
93G09	14	8 Mar-11 Jun 1993	09:05	3
93G10	17	10 Mar-21 Jun 1993	09:00	5
93G11	11	9 Mar-8 Jul 1993	10:35	(3)
93G13	15	18 Mar-3 Jul 1993	06:00	(2)
93G15	14	27 Mar-8 Jun 1993	08:30	(2)
93G17	11	16 Apr-17 Jun 1993	09:15	(3)
93G18	16	1 Apr-18 Jun 1993	08:15	3
93G19	24	30 Mar-30 Jun 1993	09:15	4
94G01	23	4 Mar-18 Jul 1994	10:50	4
94G02	19	10 Mar-11 Jul 1994	10:50	3
94G03	10	15 Mar-19 May 1994	14:05	(2)
94G07	20	4 Apr-28 Jul 1994	12:35	2
94G08	27	25 Feb-15 Jul 1994	07:45	4
94G09	25	28 Feb-27 Jul 1994	07:30	2
94G11	31	1 Mar-3 Jul 1994	14:00	2
94G12	31	15 Mar-3 Jul 1994	14:00	2
94G13	21	21 Mar-29 Jul 1994	11:15	2
94G14	9	23 Mar-25 May 1994	08:25	(1)

[a] Total number of dates used in analysis after data restrictions. See Methods for further discussion.

[b] Number of nests initiated during indicated observation period. Values in parentheses represent minimum counts; others are believed to represent the total number of nests begun. See Methods for further discussion.

on each date at approximately 5- and 10-minute intervals. Calculation of eccentricity values was based on CALHOME plots of each data subset and the bivariate normal method of Jennrich and Turner (1969). We used critical values as determined at $P = 0.25$ for a bivariate normal distribution (Swihart and Slade 1985).

To examine four potential practical approaches to the problem of dependence of successive observations, we used CALHOME to calculate the 90% and 75% adaptive-kernel contours on four distinct subsets of our data (created after application of the exclusions described above). At one extreme we included all records available from each date regardless of their temporal spacing or daily differences in sample sizes (ALL_OBS). Next, we ensured uniformity of sample sizes among dates by randomly selecting five observations per date; no concern was given to the temporal spacing of the selected points (5RANDOM). Third, we systematically selected three observations per date, with each point separated from the preceding point by an interval of ≥20 minutes (20MIN_3). Last, at the cost of reducing sample size, we randomly selected one observation point per day (1RANDOM) as our best effort to ensure data independence. Effects of grid-cell density were examined by comparing results based on a fixed 25-m grid-cell size with those obtained through CALHOME's default setting of a 30-cell by 30-cell grid scaled to each data set.

Finally, use-area boundaries (based on the adaptive-kernel method, 75% and 90% contours) were calculated from observations limited to those during 16 complete nesting cycles known to have resulted in the successful fledging of young. We defined the duration of each phase of the breeding cycle as follows: nest-building, 6 days; egg-laying, 4 days; incubation, 14 days; nestling care, 16 days; fledgling period preceding dispersal from natal territory, 21 days (Atwood 1993). The approximate schedule of each successful nest was extrapolated from dates of observed nest building, egg laying, hatching, or fledging, or from the estimated age of nestlings on a given date. In other words, for each successful nest, we established an approximately 60-day window that we estimated to encompass a single, entire breeding cycle, and used observations within that period as the basis for our analysis of use area. This idealized schedule is not meant to be interpreted rigidly; we recognize that the timing of different gnatcatcher nesting attempts may show substantial variation. Nonetheless, for our purposes here, we used this approach to reduce the possible confounding effects that gross differences in sampling duration might have on our results.

RESULTS

Independence of Data Points

Of 20 randomly selected dates in which all successive observations were used [mean time between observations 7.5 minutes, standard deviation (SD) 3.9], the null hypothesis of data independence was rejected in 14 instances (70%) (Table 2) according to the criteria of Swihart and Slade (1985). When alternating observations were used, increasing the mean time between points to 13.5 minutes (SD 5.8), the number of samples with dependent successive records decreased to 9 (45%) (Table 2). Thus, while longer intervals reduced the degree of dependence of successive observations, the improvement was far from complete.

Because of limitations in our sample sizes, we were unable to examine the effect that further increases in the length of time separating observation points might have had on data independence. Consequently, we did not identify a minimum interval at which successive observations would meet the assumptions of data independence required by standard methods of statistically analyzing animals' use areas.

Data Subsets with Varying Levels of Observation Independence

We found no significant differences among estimates of gnatcatcher use areas based on adaptive-kernel analysis (90% point contour) of four different subsets of the data ($P > 0.10$, Kruskal–Wallis test), where observations were assumed to range from highly intercorrelated (ALL_OBS) to independent (1RANDOM) (Figure 1). Harmonic-mean estimates (90% point contour) and 100% minimum convex polygons did differ significantly ($P < 0.01$, Kruskal–

Table 2 Evaluation of Independence of Successive Locations of California Gnatcatchers Recorded at Approximately 5- and 10-Minute Intervals on 20 Randomly Selected Dates

		5-Minute minimum			10-Minute minimum		
Pair	Date	Mean interval[a]	n[b]	t^2/r^2[c]	Mean interval[d]	n[b]	t^2/r^2[c]
93G04	23 Apr 1993	5	10	1.57[e]	10	5	2.07
93G04	14 May 1993	10	10	1.47[e]	15	7	2.21
93G05	30 Jun 1993	5	10	1.27[e]	11	5	0.71[e]
93G07	30 Mar 1993	18	10	1.38[e]	21	5	2.51
93G07	28 May 1993	15	10	2.07	26	6	2.19
93G07	29 Jun 1993	5	11	2.16	10	6	2.13
93G09	21 Apr 1993	5	12	1.90	11	6	3.12
93G11	24 May 1993	7	10	1.23	10	7	1.39[e]
93G13	22 Mar 1993	8	10	1.20[e]	16	6	1.88
93G13	14 Apr 1993	5	11	0.53[e]	10	6	1.06[e]
93G15	9 Apr 1993	8	10	2.09	14	6	1.23[e]
93G19	16 Apr 1993	5	10	1.65[e]	10	5	2.17
93G19	10 Jun 1993	5	10	0.87[e]	10	5	1.11[e]
94G01	18 July 1994	14	11	0.75[e]	30	5	1.70
94G09	27 Jun 1994	5	10	1.89	10	5	2.24
94G11	30 Jun 1994	6	11	0.63[e]	13	6	1.23[e]
94G12	5 Apr 1994	8	11	0.90[e]	11	8	1.29[e]
94G12	26 Apr 1994	5	10	0.33[e]	10	6	0.71[e]
94G13	6 Jun 1994	5	10	1.92	11	5	1.34[e]
94G14	4 Apr 1994	5	10	1.42[e]	10	5	3.01

[a] Mean time (minutes) between successive observations, using all points obtained at minimum intervals of 5 minutes.

[b] Number of observation points separated by indicated minimum interval (number of pairs of successive observations = $n - 1$).

[c] Schoener's ratio, mean squared distance between successive observations/mean squared distance from center of activity.

[d] Mean time (minutes) between successive observations, using alternate points obtained at minimum intervals of 10 minutes.

[e] Instances where successive data points were dependent ($P = 0.25$, bivariate uniform distribution) according to the criteria of Swihart and Slade (1985).

Wallis test) among the four data subsets, with both methods yielding progressively smaller use-area estimates as sample sizes were reduced by increasingly stringent efforts to achieve data independence (Figure 1).

Different Analytic Methods

We found significant differences ($P < 0.01$, paired t test) between estimates of gnatcatcher use areas based on adaptive-kernel and harmonic-mean methods using both the 90% and 75% point contours (Table 3). Estimates based on the harmonic mean were, on average, approximately 13% smaller than those obtained by the adaptive-kernel method at both contour levels. Similarly, results based on the 90% adaptive kernel and 90%

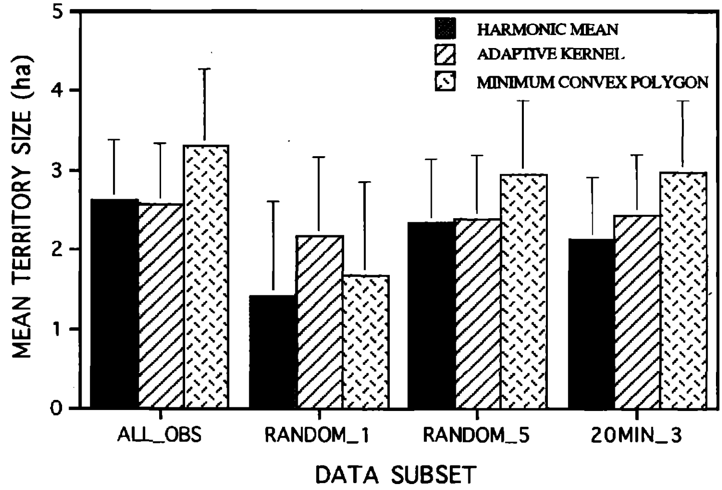

Figure 1. Mean estimates of California Gnatcatcher use areas based on four subsets of data from the Palos Verdes Peninsula. Values based on (A) adaptive-kernel 90% point contour, (B) harmonic-mean 90% point contours, and (C) 100% minimum convex polygon. Error bars, 2 standard errors. See Methods for procedures used to select different data subsets.

harmonic mean were significantly smaller than those provided by the 100% minimum convex polygon ($P < 0.01$, paired t test); however, the magnitude of these expected differences, especially with the adaptive-kernel method, was relatively minor [90% adaptive kernel = 85% (mean) of minimum convex polygon; 90% harmonic mean = 75% (mean) of minimum convex polygon]. In 7 (28%) of 25 instances the 90% adaptive-kernel method estimated use areas that exceeded the 100% minimum convex polygon; in only two instances (8%) did the 90% harmonic-mean method predict use-area boundaries greater than the minimum convex polygon. All methods yielded approximately comparable coefficients of variation (Table 3).

Variation in Grid-Cell Density

We found no significant differences between use-area estimates derived from CALHOME's default setting (a 30-cell by 30-cell grid scaled to each data set) and a fixed 25-m grid-cell size for either the adaptive-kernel ($P > 0.10$, paired t test) or harmonic-mean ($P = 0.10$, paired t test) methods.

Differences in Duration of Sampling

Estimates of gnatcatcher use areas based on observations during 16 successful nesting attempts (nest building through departure of fledglings from natal territory) were significantly smaller than estimates of areas used by these same pairs throughout the entire breeding season ($P < 0.01$, paired t test; Table 4). Within each successful nesting attempt, the number of sampling dates influenced both minimum-convex-polygon (100%) and adap-

Table 3 Estimates of California Gnatcatcher Use Areas Based on Three Methods of Data Analysis

Pair	*n*[a]	Use-area estimate (ha)				
		75% contour		90% contour		100%
		Adaptive kernel	Harmonic mean	Adaptive kernel	Harmonic mean	Minimum convex polygon
93G01	39	2.05	1.57	3.59	3.38	4.05
93G02	72	1.12	0.99	2.38	1.95	2.51
93G03	66	1.29	1.08	2.39	2.23	3.11
93G05	90	0.49	0.41	1.55	1.38	4.24
93G06	84	2.22	2.17	3.77	3.47	5.51
93G07	87	0.75	0.77	1.34	1.35	1.29
93G09	42	1.24	1.10	2.41	2.21	2.16
93G10	54	0.99	0.94	1.60	1.63	2.16
93G11	33	0.75	0.79	1.93	1.57	1.81
93G13	45	1.86	1.71	4.87	3.60	5.65
93G15	42	1.21	1.13	2.05	1.40	1.71
93G17	30	0.61	0.63	2.45	1.22	1.38
93G18	48	1.05	0.96	2.70	1.84	2.61
93G19	69	2.17	1.51	3.49	3.48	3.52
93G42	114	1.08	1.04	2.27	2.18	3.17
94G01	72	1.37	1.15	2.55	2.31	3.71
94G02	57	1.51	1.30	2.52	1.89	3.76
94G03	30	0.46	0.39	0.99	0.90	1.05
94G07	63	0.61	0.58	1.04	0.86	0.96
94G08	78	2.01	1.99	3.79	3.64	4.68
94G09	72	1.69	1.32	3.12	2.95	4.62
94G11	102	1.17	1.15	1.88	2.07	3.33
94G12	99	1.35	1.18	2.20	2.23	2.87
94G13	63	1.26	1.24	2.00	1.88	2.11
94G14	30	1.43	1.22	1.71	1.73	1.93
Mean		1.27	1.13	2.42	2.13	2.96
Standard deviation		0.52	0.44	0.93	0.84	1.34
Coefficient of variation		40.6	38.4	38.4	39.4	45.4

[a] Sample size based on data subset consisting of observations separated by intervals of ≥20 min. See Methods for further discussion.

tive-kernel (90%) estimates of use-area size (Figure 2). Estimates of use area based on the minimum-convex-polygon method showed incremental increases even after 8 days of sampling. Although the sample size is small ($n = 10$ successful nests represented by at least 10 sample dates), estimates of use areas based on the adaptive-kernel method appeared to equilibrate more quickly, with only a 5% difference in mean estimates obtained from 6 as opposed to 10 days of sampling effort (Figure 2).

On the Palos Verdes Peninsula, California Gnatcatcher territory sizes during single successful nesting attempts varied from 0.6 to 2.5 ha (mean 1.52 ha, SD 0.60) (Table 4).

Table 4 Areas Used by California Gnatcatchers while Nesting[a] and over Entire Breeding Season

	n		Use-area estimate (ha)[b]	
Pair	Successful cycle	Entire season	Successful cycle	Entire season
93G02	42	72	2.03	2.38
93G03	30	66	0.82	2.39
93G05	27	90	1.62	1.55
93G06	42	84	2.09	3.77
93G07	33	87	0.62	1.34
93G09	21	42	1.57	2.41
93G11	21	33	1.08	1.93
93G15	30	42	1.65	2.05
93G18	36	48	1.91	2.70
93G19	27	69	2.37	3.49
94G02	24	57	0.79	2.52
94G07	33	63	0.70	1.04
94G09	24	72	2.54	3.12
94G11	45	102	1.42	1.88
94G12	45	99	1.83	2.20
94G13	33	63	1.34	2.00
Mean (SD)			1.52 (0.60)	2.29 (0.73)

[a] Based on observatons during single, successful nesting attempts (nest building through dispersal of fledglings).

[b] Based on adaptive-kernel method (90% point contour), 25-m grid cells.

DISCUSSION

Size estimates of California Gnatcatcher use areas can be influenced by differences in methods of both data collection and data analysis. From observations of breeding birds on the Palos Verdes Peninsula, we found that localities recorded at intervals of 10 minutes or less were often spatially correlated and therefore likely to violate the assumption of data independence inherent to most statistical models of animal use areas (Swihart and Slade 1985). Duration of the data-collection period may also influence use-area estimates. Areas used during a single successful nesting cycle (nest building through fledging) were smaller than estimates of areas used by the same pairs throughout the entire breeding season. Even within a single nesting cycle, the number of visits to a site may influence estimates of use area. The results presented here, based on the adaptive-kernel method provided by CALHOME, suggest that at least six visits are needed before there is any evident stabilization of use-area estimates. Further study regarding the minimum number of visits required to estimate the boundaries of gnatcatcher use areas accurately is warranted.

Various quantitative methods may also yield different estimates of California Gnatcatcher use areas; Lawson and Rodgers (1997) even found that different software packages produced variable results for the same home-range estimator. Using CALHOME, we obtained significant differences

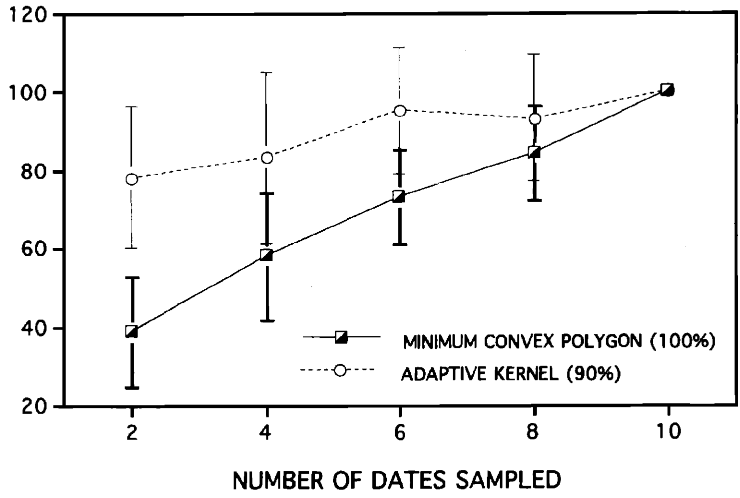

Figure 2. Minimum-convex-polygon and adaptive-kernel estimates of California Gnatcatcher use areas by number of sampling dates. Estimates expressed as percentage of value derived from data collected on 10 dates. Error bars, 2 standard errors.

between estimates of use areas based on two nonparametric, probabilistic methods (adaptive kernel and harmonic mean), as well as between values derived by either of these methods and those obtained by the minimum-convex-polygon approach. Furthermore, results from both the adaptive-kernel and harmonic-mean methods may be affected by the dimensions of the grid cells applied in the analysis; Kie et al. (1994) noted that the adaptive-kernel model is less sensitive to the effects of different grid-cell sizes than the harmonic mean. These authors concluded that "we do not recommend the harmonic-mean method of home-range analysis. It has been shown to be an improper form of the statistical method of kernel estimation."

Since the early 1990s several studies of California Gnatcatcher territory or home-range size have been presented in unpublished reports, usually in the context of environmental reviews required for approval of a development. Many of these preliminary documents have lacked detailed descriptions of field and analytic techniques, making it difficult to compare the results of different studies. Compounding this problem is the fact that work aimed at satisfying regulatory requirements, in which all movements of a pair throughout an entire year might legitimately be considered of interest, are fundamentally different from studies focused on examining whether territory size is correlated with some measure of habitat quality. The spread of home-range sizes reported during a single breeding season, from 1 ha (this study) to over 15 ha (ERCE, unpubl. data cited by Atwood 1993), suggests to us a degree of variability exceeding what we would expect solely on the basis of habitat differences. At least some of this variation may reflect differing methods of data collection and analysis.

Consequently, we caution against confident assertions about the area required for California Gnatcatcher territories or home ranges. While we believe that use-area boundaries may be effectively identified by experienced workers without use of computer models or concern over issues such as data independence, and that such delineations may be adequate (or even superior) for use in management or regulatory decisions, we do not think that subjectively mapped polygons will yield data that permit testing hypotheses about the possible relationship between habitat quality and gnatcatcher territory size. Without more rigorously collected data and more careful descriptions of the methods used to analyze such information, our understanding of the California Gnatcatcher's home-range requirements will remain confused and uncertain.

Finally, we advise that care be taken in attempts to delineate boundaries of gnatcatcher use areas in documents intended for nonscientific audiences. Such presentations may easily be misinterpreted as implying a degree of territory permanence that ignores seasonal and annual variability and a level of certainty in placement of lines on a map that exceeds what was actually observed in the field. Instead, we suggest that the dynamic nature of California Gnatcatcher home ranges and breeding territories requires that land-use planners and regulatory authorities consider all areas of coastal sage scrub near sites recently occupied by the species to be of potential conservation value.

SUMMARY

Estimates of California Gnatcatcher territory size may be influenced by differences in data collection and analyses. Recording localities of birds at intervals of 10 minutes or less frequently violated the assumption of data independence basic to most statistical models of animal use areas. The number of dates on which observations were collected also influenced estimates of use area. We compared the results of two nonparametric methods of predicting animal home ranges (adaptive kernel and harmonic mean) with each other, and with results obtained by the nonprobabilistic approach of calculating the minimum convex polygon. We recommend that studies of gnatcatcher territory size (1) be based on observations at intervals of not less than 20 minutes, (2) include observations on at least six dates within a sampling window beginning with nest building and ending within 3 weeks of fledging, and (3) present results derived from a variety of objective, quantitative models, including the adaptive-kernel, harmonic-mean, and minimum-convex-polygon methods. Reports describing such studies should also detail the methods used in obtaining and analyzing data, including, for studies during the breeding season, information about the number of nesting attempts during the period of data collection.

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LITERATURE CITED

Akçakaya, H. R., and Atwood, J. L. 1997. A habitat-based metapopulation model of the California Gnatcatcher. Cons. Biol. 11:422–434.

Atwood, J. L. 1993. California Gnatcatchers and coastal sage scrub: The biological basis for endangered species listing, in Interface between Ecology and Land Development in California (J. E. Keeley, ed.), pp. 149-169. S. Calif. Acad. Sci., Los Angeles.

Atwood, J. L., and Noss, R. F. 1994. Gnatcatchers and development: A "train wreck" avoided? Illahee 10:123–132.

Bean, M. J., Fitzgerald, S. G., and O'Connell, M. A. 1991. Reconciling Conflicts under the Endangered Species Act: The Habitat Planning Experience. World Wildlife Fund, Washington, D.C.

Dixon, K. R., and Chapman, J. A. 1980. Harmonic-mean measure of animal activity areas. Ecology 61:1040–1044.

Jennrich, R. I., and Turner, F. B. 1969. Measurement of non-circular home range. J. Theor. Biol. 22:227–237.

Kie, J. G., Baldwin, J. A., and Evans, C. J. 1994. CALHOME: Home Range Analysis Program electronic user's manual. U.S. Forest Service, Pac. Southwest Res. Sta., Fresno.

Larkin, R. P., and Halkin, D. 1994. A review of software packages for estimating animal home ranges. Wildlife Soc. Bull. 22:274–287.

Lawson, E. J. G., and Rodgers, A. R. 1997. Differences in home-range size computed in commonly used software programs. Wildlife Soc. Bull. 25:721–729.

Mohr, C. O. 1947. Table of equivalent populations of North American mammals. Am. Midland Nat. 37:223–249.

Reid, T. S., and Murphy, D. D. 1995. Providing a regional context for local conservation action. BioScience Suppl. 1995 (Science and Biodiversity Policy):84–90.

Swihart, R. K., and Slade, N. A. 1985. Testing for independence of observations in animal movements. Ecology 66:1176–1184.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

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