ESTIMATING THE NUMBER OF TERRITORIAL MALES IN LOW-DENSITY POPULATIONS OF THE SOOTY GROUSE

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ABSTRACT: Sierra Sooty Grouse (*Dendragapus fuliginosus sierrae*) are challenging to census because they occur at low densities, are cryptically colored, and live quietly in the forest canopy most of the year. I developed a census method that accounts for several aspects of Sierra Sooty Grouse breeding biology that hinder accurate estimates, including seasonality of singing, anomalous singing by yearling males, low population density, and clumped dispersion of breeding males. Within 167 km^2 near Pinecrest, Tuolumne County, California, I conducted landscape-scale censuses along a network of line transects from 2006 to 2009 and detected 22 clusters of breeding males (hooting groups). I then used spot-mapping methods to estimate the number of individual males within hooting groups. Territorial display by transient (yearling) males lasted only a few days and became uncommon after 1 May; persistently territorial males became increasingly reluctant to display after mid-May. Thus limiting the census period to 1 May–15 June maximizes detections of persistently territorial males, and a minimum interval of 5 days between repeated censuses minimizes misidentification of transient males as territorial. In the 13 hooting groups that I spot-mapped, the number of persistently territorial males averaged 4.9, and the distance from the center of a territory to the center of the nearest neighboring territory averaged 209 m. The probability of a persistently territorial male being detected on a single census visit averaged 0.71. Three repetitions of the group-scale census within a hooting season were sufficient to detect 98% of persistently territorial males. The density of territorial males was much lower (~0.6 male/km^2), and the distribution of males' territories was much more clumped, than reported in other regions. The number of persistently territorial males was static from 2009 to 2011.

There is no standardized widely used method for censusing the Sooty Grouse (*Dendragapus fuliginosus*), although many censuses have been undertaken on an *ad hoc* basis. Agencies mandated to monitor Sierra Sooty Grouse (*D. f. sierrae*) require efficient, unbiased methods of census. This subspecies is difficult to census because the birds are cryptic and remain quietly in the forest canopy most of the year, the population density is low, the distribution of breeding males is clumped, the frequency of song varies through the breeding season, and occasionally yearling males display territorially. I developed auditory census methods that account for these aspects of the grouse's breeding biology and used them in repeated censuses in Tuolumne County in 2009 and 2011.

The Sierra Sooty Grouse occupies relatively open and arid forests, unlike most of the other subspecies of the Sooty Grouse, which typically occupy humid coastal forests (Bendell and Zwickel 1984). Population densities of *D. f. sierrae* are also lower (Bendell and Zwickel 1984, Zwickel and Bendell 2004), and the subspecies is more arboreal than the others (most males' breeding display occurs in the forest canopy). Bland and Gardner (2013) found that the Sierra Sooty Grouse is closely associated with large trees and mature forest, with an open canopy. Where forest cover is open and population densities are low, male Sooty Grouse congregate in spring at traditional

breeding sites (Lewis 1985a), forming what Bendell and Elliott (1967) called hooting groups. Available evidence indicates this is the case throughout the range of the Sierra Sooty Grouse (Bland 1993, unpubl. data). Zwickel and Bendell (2004:157) reported that hooting groups usually consist of 2 or 3 males but can include up to 7 or 8. Hooting groups are not considered classical leks, primarily because they lack a communal display arena (Lewis 1985a). The locations of individuals' territories, and by extension hooting areas, vary little from year to year (Bendell 1955, McNicholl 1978) or from generation to generation (males can live ≥14 years, Zwickel et al. 1989), until the group dies out or vegetation succession makes the site unsuitable (Zwickel and Bendell 1985). The clumped distribution of breeding males constrains the methods and efficiency of a census. Large areas of apparently suitable breeding habitat may be unoccupied and so unproductive to census. Conversely, detection of a single hooting male readily leads to detection of the other territorial males in a group because all engage in countersinging (Zwickel and Bendell 2004:157).

In the Sierra Nevada, peak hooting occurs between mid-April and early June (Zwickel and Bendell 2004:156, Bland unpubl. data). During this period, territorial males usually hoot throughout the day, with peaks in hooting around sunrise and sunset (Bendell 1955, Stewart 1967, McNicholl 1978, Zwickel and Bendell 2004). Hooting is often audible at distances up to 500 m (Hjorth 1970) and up to 1 km when the sound is not attenuated by topography or air movement (Doerr at al. 1984, Bland unpubl. data). Quiet or resting territorial males hoot or flutter their wings in response to broadcast of recorded calls of a female (Stirling and Bendell 1966, McNicholl 1981, Niederleitner 1987) and to a human observer's intrusion into their territory (Zwickel and Bendell 2004:160), unless startled or threatened by the observer. Early in the hooting season, a few nonterritorial males (yearlings and nonterritorial adults, Zwickel and Bendell 2004:154) also hoot for a few days, potentially inflating early-season counts of territorial males (McNicholl 1981). I refer to these as transient males, as opposed to persistently territorial males. Late in the hooting season, quiet or resting territorial males become reluctant to respond to recorded calls of a female (McNicholl 1981) or intrusions by observers, potentially deflating late-season counts based on calls.

There have been three previous censuses of the Sierra Sooty Grouse. Hoffmann (1956) conducted a repeated census at Sagehen Creek, but his results are doubtful because of his informal method and small sample size (≤6 males). Bendell and Zwickel (1984) ranked Sooty Grouse densities on a subjective 0–5 scale at two locations. Bland (1993) counted the number of territorial males within hooting groups at six locations.

Outside California, most published Sooty Grouse censuses have been based on labor-intensive banding or area searches, with the objective of achieving a total count (Bendell 1955, Bendell and Elliott 1967, Boag 1966, Donaldson and Bergerud 1974, Redfield 1975, Zwickel and Bendell 2004). The effort required to complete such censuses is difficult to determine in advance because it is predicated on gradual depletion of undetected individuals. The roadside "call counts" conducted by some state game agencies are indices of populations of adult males at regional scales and are generally capable of detecting only large changes or differences (Zwickel 1982, Fox

et al. 2009). Zwickel (1982) provided the basic outline for an audio census of male Sooty Grouse but offered few procedural details. There remains a need for an efficient, standardized method for censusing the Sooty Grouse. The California Department of Fish and Wildlife (CDFW) requires population data for establishing bag limits for the Sooty Grouse and monitoring populations thought to be in decline, and the U.S. Forest Service (USFS) requires such data to support its bioregional Management Indicator Species program (USFS 2008).

The objectives of this paper are to present my findings on aspects of the Sooty Grouse's breeding biology that affect auditory censuses, describe my census procedures, and report the results of a repeated census and estimate of density. My census protocol could be adopted by agencies for local-scale monitoring, and the supporting research could serve as a methodological foundation for developing probabilistic census methods or monitoring programs at a regional scale.

STUDY AREA

My censuses took place in an area of 167 km² centered near Pinecrest Peak, Stanislaus National Forest, Tuolumne County, California (38° 14′ N, 119° 56′ W), on the western slope of the Sierra Nevada (Figure 1). Peaks and ridges within the area reach 2600–2800 m elevation. I set the lower boundary of the study area at 1775 m elevation, ~360 m below the presumed lower limit of grouse in the region (Grinnell et al. 1918). In this area, the predominant forest types include Sierran mixed-conifer forest (<~2200 m), red fir (*Abies magnifica*) forest (~2200–2700 m), and lodgepole pine (*Pinus contorta*)/subalpine conifer forest (>~2700 m). The eastern third of the study area lies within Emigrant Wilderness Area and is relatively pristine. Elsewhere, logging, including clear-cutting, has been widespread but generally at a small scale (1–10 ha). The entire area is usually covered with 1–4 m of snow from late November through early April, and in 2011 it received unusually high snowfall (153% of normal in April, Cooperative Snow Survey, California Department of Water Resources).

METHODS

My census methods incorporate two complementary procedures, one for counting groups of hooting grouse at the landscape scale (landscape-scale transects), another for counting individual grouse within those groups (group-scale transects). I controlled for observers' variability in skill and acuity of hearing by limiting the number of observers (four for landscape-scale censuses, three for group-scale censuses) and mentoring each observer on his or her first two censuses.

Landscape-Scale Census

Landscape-scale censuses extended from 15 April to 7 June, 2006–2009, along a network of line transects that intersected all forested portions of the study area (Figure 1). I laid out landscape-scale transects with GIS software
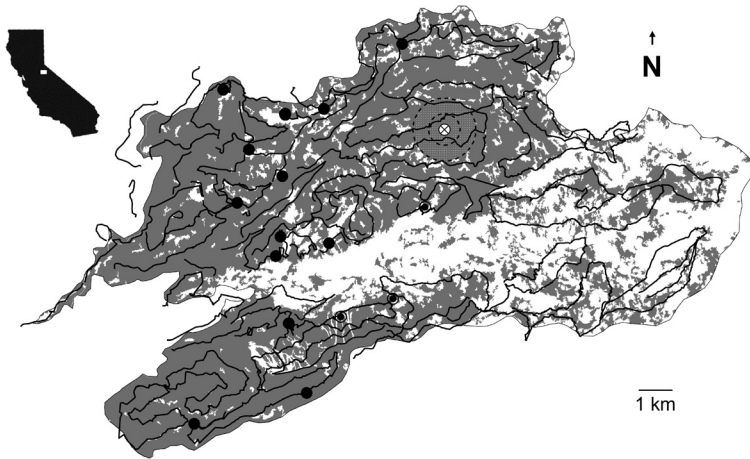
Figure 1. Pinecrest study area. Shaded area indicates ≥10 % forest cover; solid lines, landscape-scale census transects; circles enclosing stars, hooting groups censused in both 2009 and 2011; circles enclosing dots, hooting groups censused in 2009 only; solid dots, hooting groups assessed by area searches or incomplete censuses, 2006–2009; circle enclosing an ×, a hypothetical hooting male, surrounded by gridded areas representing maximum distances of audibility of 500 m (Hjorth 1970) and 1000 m (Doerr et al. 1984).

(Manifold version 8, Manifold Software Limited, Hong Kong) by drawing them over a topographic map of the study area. Each transect was drawn to minimize loss or gain of elevation, skirt dangerous cliffs and streams, and be traversable by foot within 4–6 hours (often by snowshoe). Adjacent transects, and parallel portions of loop transects, were spaced ~400–800 m apart (measured as horizontal distance on a map) to ensure that more than one transect would fall within the range (~500–1000 m) of audibility of hooting grouse located anywhere in forested portions of the study area (Figure 1). Transect routes were downloaded to hand-held Global Positioning System (GPS) units (Model GPSMAP 60CSx, Garmin International, Inc., Olathe, KS), which were used in the field so that the predetermined routes could be navigated as closely as possible. A single observer walked each transect once, stopping every 300–500 m at prominent spurs or vantage points to listen for hooting grouse. If no hooting was audible, the observer broadcast a recorded 22-syllable cackle of a female (provided by J. Bendell, Univ. Toronto) in each cardinal direction by using an MP3 audio player (Model SA4111, Philips Electronics, Andover, MA) and amplifying speakers (Model 40-1441, Radio Shack, Fort Worth, TX).

Where hooting was detected, the observer did an area search to locate as many displaying grouse in the area as possible, using recorded calls of a female when necessary to re-initiate display. I defined a hooting group as all males a person could hear displaying from at least one previously detected grouse's territory (this definition works well where grouse densities are low

and predominant ridges are parallel, but it does not perform as well where densities are higher or ridges converge in a tight "U"). I considered both hooting and wing-fluttering to be territorial display behavior (Zwickel and Bendell 2004). The observer recorded coordinates of displaying grouse with a hand-held GPS unit while standing beneath the grouse's songpost tree. If a displaying grouse could not be observed directly because of obstructing foliage, the location of its apparent songpost tree was recorded. Later I used location coordinates to lay out group-scale transects in GIS, as described below. After recording locations of all displaying grouse at the site, the observer continued along the landscape-scale transect. Landscape-scale censuses were conducted during all daylight hours, except during storms or when air movement was strong enough to attenuate or obscure distant display sounds.

Group-Scale Census

I also laid out group-scale transects in advance with GIS, using locations of displaying grouse recorded during landscape-scale censuses. Each group-scale transect was positioned on a georeferenced orthophotograph (digital orthophoto quarter quadrangle, Stanislaus National Forest). I then centered a transparent 100-m grid, with total dimensions of 1500×1500 m (an area slightly larger than the area occupied by a typical hooting group), over the locations of the grouse in the hooting group, then trimmed the photograph to the 1500×1500 m grid to create a map of the hooting group. I labeled the grid lines with the applicable Universal Transverse Mercator values and drew a group-scale transect line on the map so that it (1) wove through successive territories, passing by known songposts at a distance of ~50–100 m, and (2) maintained a curtain of tree foliage between the observer and all known songposts. In 2011, the year of the second census, I also ensured that transects extended 100 m beyond the furthest known territory at each end of a transect, thereby positioning observers where any additional territorial males would likely be detected—territories that constitute a hooting group are typically distributed more or less linearly along an elevation contour (Bland and Gardner 2013). Transect routes were downloaded to hand-held GPS units, which observers used in the field to navigate the predetermined routes.

An observer slowly walked the full length of a group-scale transect (larger groups required longer transects), then retraced it in the opposite direction. The initial pass served to rouse as many individuals as possible into heightened territoriality and display. Where no hooting was audible within 200–300 m, the observer broadcast one or two cackle calls at ~150-m intervals to induce any nearby silent males to display (excessive use of recorded calls can cause males to move, complicating spot-map analysis). If a displaying male was not visible from the transect (obscured by foliage), the observer estimated its location from the locations of display sounds from a series of points along the transect. Estimated locations are acceptable for such counts because males' territories are exclusive and typically encompass 0.6–2.1 ha (Zwickel and Bendell 2004:200). If necessary, unresponsive males were approached unobtrusively to no closer than ~75 m and stimulated with a recorded cackle call of a female. Visual contact was avoided to ensure continued hooting, which increases display (hence, detection) of additional males (McNicholl 1978). Locations of displaying grouse were

marked by hand onto the hooting-group map. When an observer was uncertain whether a truncated hoot sequence or quick wing-flutter might have been detected, he or she noted the location on the hooting-group map as a possible detection. Songpost trees were usually distinguishable on aerial photographs by their large size. Group-scale censuses took place between 08:00 and 14:00, and occasionally in late afternoon, but never during storms or when a continuous strong wind would have attenuated or obscured display sounds. Prior to a repetition of a group-scale census, I realigned transect lines where necessary so that they passed within 50–100 m of newly detected territories and maintained a curtain of tree foliage between the observer and all known songposts.

In 2009, I conducted group-scale censuses of 15 hooting groups on five occasions between 19 April and 9 June, 2009. The average interval between these censuses was 8.3 days and the minimum was 3 days, except for 1 day on one occasion and 2 on another. Five additional groups were censused only 1–4 times because of limited manpower, and 2 were assessed only by initial area searches during landscape-scale censuses (these 7 groups were omitted from group-scale analyses). In 2011, I conducted group-scale censuses from 4 May to 16 June at 11 of the 15 hooting groups censused in 2009.

Census Timing

A primary objective of the 2009 group-scale censuses was to document patterns of hooting activity through the peak hooting period, in order to determine the optimal period and time of day for future censuses. To identify when anomalous hooting by transient males was most frequent, I compared the frequency of one-time detections (transient males cease displaying after a few days) across a series of 10-day intervals. To determine the approximate date when persistently territorial males became too reluctant to display to be censused reliably, I analyzed the proportion of males detected only on return runs of censuses (were responsive only after neighboring males had been roused into display).

Data Analysis

I estimated the number of persistently territorial males constituting hooting groups with standard spot-mapping methods (Kendeigh 1944): by plotting detection locations on repeated censuses, identifying clusters of detections (within areas equal to a typical territory, ~1.5 ha), and using records of simultaneous singing to distinguish between two or more adjacent territories. I considered males that displayed on any two repetitions of a group-scale census to be persistently territorial. I estimated territory centers from mean locations of spot-map detections, and hooting-group centers from mean locations of territory centers. I used Clark and Evans' (1954) nearest-neighbor method to assess the distribution of males' territories because it has been used in studies of the Sooty Grouse previously published. Clark and Evans' R provides a measure of the degree to which observed distribution patterns deviate from a randomly distributed population of equal density, where values range from zero to 2.1491, with zero indicating maximum clumping, one random spacing, and 2.1491 even spacing.

It was not feasible to estimate territory size because five repetitions of group-scale censuses resulted in too few detection locations. Instead, I measured the maximum spread of detection points attributed to each territorial male, which served as a rough index of territory size. This was helpful for distinguishing between (tallying) territories on spot maps because detections that were too widely dispersed were unlikely to be from a single persistently territorial male during peak hooting season, although activity areas do expand after peak hooting season (Lewis 1985b, Bland unpubl. data).

When analyzing the probability of detection, I considered each census visit to a persistently territorial male to be an experimental trial. I estimated cumulative detection probability as $P^* = 1 - (\Pi^K 1 - p_j)$, where K = the number of census repetitions, and p = the probability of detection on census repetition j (MacKenzie et al. 2005). I used a chi-squared test to assess whether time of day (before 11:00 versus after 11:00) influenced detection rates.

In order to determine the minimum number of census visits and minimum time interval between visits, I analyzed the 2009 group-scale data by using only three of the five repetitions of a census (four when it was necessary to determine if a male that had displayed on only the second or third census had persisted). I omitted census repetitions conducted earlier than 1 May, later than 15 June, and <5 days after a previous census (2 of the 15 hooting groups had to be omitted from this analysis because the number or timing of repetitions of the census could not be reconciled with the revised criteria). Because this approach proved to be effective and efficient (see Results), I used it for censuses in 2011 and to analyze census data from both years.

RESULTS

Landscape-Scale Census

I detected 22 hooting groups in the study area, along 500 km of landscape-scale transects. The average distance between the center of a group to that of the nearest neighboring group was 1916 m (range 1239–3676 m, SD = 680).

Group-Scale Detection Rates and Timing

The probability of an individual territorial male being detected on a single census visit averaged 0.71 (2009 census, 3 repetitions, 61 individuals [2 omitted, see footnote e in Table 1], range 0.33–1.0, SD = 0.24). The cumulative probability of detection was 0.92 after the second repetition, 0.98 after the third repetition, and 0.99 after the fourth repetition. Persistently territorial males were equally detectable before and after 11:00 ($\chi^2 = 0.273$, $P = 0.60$; 195 trials between 07:00 and 10:59, 161 trials between 11:00 and 18:00). Because detection rates were high, three or four repetitions were sufficient to detect all, or nearly all, persistently territorial males (Figure 2).

In 2009, I started group-scale censuses early in the hooting season (19 April), while display by transient males was still relatively common (McNicholl 1981). One-time detections of displaying males (presumed transients) were common in late April (23% of detections), but they declined rapidly by 1 May and remained relatively rare thereafter (5–9 % of detections, Figure 3). A start

date of 1 May therefore avoided most detections of transient males. When I specified a minimum of 3 days between censuses, four males that were detected twice within 3 days were misclassified as persistently territorial. When I specified a minimum interval between censuses of 5 days, these individuals were detected only once and so classified as transient. Persistently territorial males became increasingly reluctant to display after mid-May (Figure 3), but broadcast of calls of a female continued to stimulate them to display reliably

Table 1 Numbers of Persistently Territorial Male Sooty Grouse Estimated in 2009 and 2011

	Estimated number of persistently territorial males[a]		
Hooting group	2009 initial[b]	2009 final[c]	2011[d]
Punch Bowl	4	4	2
Pike's Peak	9	10[e, f]	7
Pinecrest Peak Trail	5	4[f, g]	6
Gooseberry	7	6[f]	7
Waterhouse Trail	8	—[h]	—[h]
Pinecrest Peak	10	10[f]	10[f]
Bull Run Rock	3	—[h]	—[h]
Herring Cr. Reservoir	2	2	3
Aspen Meadow	7	5[f]	5
Flying Horse Boneyard	6	6	4
Lift 8	2	2	—[i]
Mill Creek Ridge	3	3	3
Cow Creek	3	2	2
Mini-Gargoyles	5	5[f]	—[i]
Gargoyles	4	4	3
15-group total (mean)	78 (5.2)	—	—
13-group total (mean)	67 (5.5)	63 (4.9)	—
11-group total (mean)	—	56 (5.1)	52 (4.7)

[a]Detected on at least two repetitions of a census.

[b]Data recorded 19 April–9 June 2009, in five repetitions of the census and a minimum of 3 days between repetitions.

[c]Data limited to 1 May–9 June (as early as 28 April in two cases) 2009, in three repetitions of the census (plus a fourth when necessary to confirm persistence of individuals detected on only the second or third census) and a minimum of 5 days between repetitions (to exclude transients).

[d]Data recorded 4 May–16 June 2011, in three repetitions of the census and a minimum of 5 days between repetitions.

[e]Includes two individuals that were first detected at the periphery of the hooting group on the fifth census. Subsequent observations outside formal censuses confirmed these individuals persisted for at least two more weeks. This shortcoming in placement of transects was remedied by amending the protocol to ensure that group-scale transects extended 100 m beyond the furthest known territories at each end of a transect.

[f]One-time detection on the second or third census necessitated addition of a fourth census.

[g]Time did not permit an additional census, so an available census preceding peak hooting was used.

[h]Omitted from analysis because the 5 repetitions of the original census could not be reconciled with the criteria for number or timing of repetitions in the final protocol.

[i]Too remote to be recensused with the manpower available in 2011.

until ~15 June, so the dates for the end of the censuses I used in 2009 (9 June) and 2011 (16 June) were appropriate (also see Stirling and Bendell 1966). Anecdotally, I observed that the final decline in hooting activity appeared to coincide with late-morning temperatures rising above ~20 °C.

Unusually deep accumulation of snow did not delay peak hooting season in 2011; the likelihood of persistently territorial males being detected during the first 15 days of May (the earliest period for which data were available in both years) was actually higher in 2011 than in 2009 ($\chi^2 = 4.77$, $P = 0.029$).

Census Estimates

Without correction for census timing, the 2009 group-scale censuses resulted in an estimate of 78 persistently territorial males at 15 hooting groups (Table 1) and 17 one-time detections of transient males. Corrected for timing, the estimate for 13 of these groups (two could not be reconciled with the corrected timing) was 63 persistently territorial males (Table 1), with an average group size of 4.9 individuals (range 2–10, SD = 2.7) and 13 one-time detections of transient males. A fourth repetition of the group-scale census was necessary at 6 (46%) of the 13 groups. The average distance between centers of nearest neighboring territories within a group was 209 m (range 75–638 m, SD = 166 m), and the spread of points for an individual male averaged 85.9 m (SD = 44.0 m, 2–5 detections/individual). The 9 groups
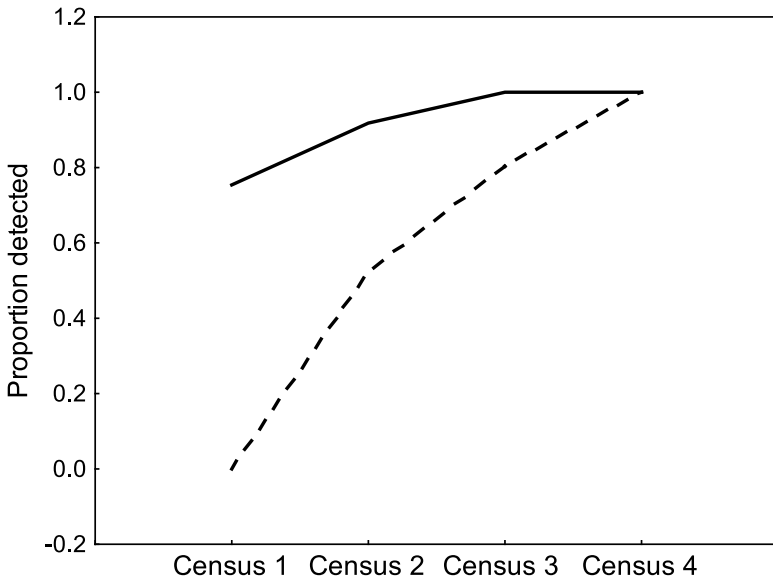

Figure 2. Proportion of persistently territorial males detected and confirmed over 4 successive censuses. Solid line represents initial detection; dashed line, second (confirmatory) detection (2009 census data, 13 hooting groups, 61 individuals [2 omitted], minimum of 5 days between each repetition of the census).
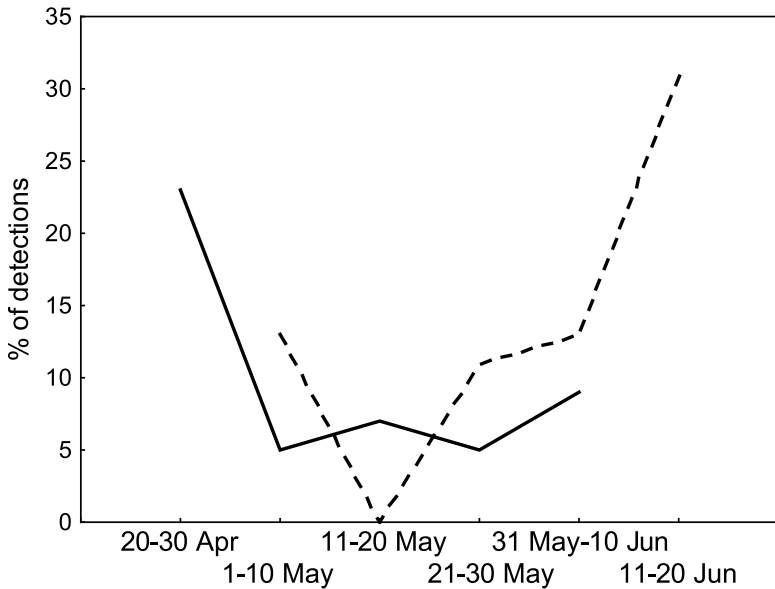
Figure 3. Seasonal patterns of propensity of transient and persistently territorial males to display (data recorded earlier in 2009 than in 2011). Solid line represents the proportion of males detected displaying on only one occasion in 2009 (presumed yearlings or nonterritorial adults); dashed line, the proportion of persistently territorial males displaying only on the return run of censuses in 2011 (after the entire group had been stimulated with broadcasts of the call of a female).

for which censuses were incomplete contained an estimated 38 territorial males, with an average group size of 4.2 individuals (range 1–11, mode = 3, SD = 3.3).

The density of breeding males across the entire 167-km^2 study area was roughly 0.6/km^2, based on the combined results of group-scale censuses at 13 groups in 2009 and area searches or incomplete censuses at the 9 remaining groups from 2006 to 2009. The distribution of males' territories (those detected by area searches, complete censuses, and incomplete censuses pooled), was highly clumped at the landscape scale ($R = 0.42$, $c = 11.12$, $P = <0.001$), although the significance of this test could be somewhat less than calculated because population size was estimated (Clark and Evans 1954).

In 2011, I recensused 11 of the 13 hooting groups censused in 2009, and estimated there were 52 persistently territorial males, a result not significantly different from the 2009 estimate for those 11 hooting groups ($\chi^2 = 0.308$, $P = 0.579$, Table 1). There were just 8 one-time detections of transient males in 2011, and a fourth census was necessary at only 1 (9%) of the groups. The similarity in 2009 and 2011 estimates suggests the Pinecrest population of the Sooty Grouse remained static over those 3 years.

DISCUSSION

Variation in Song Frequency, Detectability, and Environmental Interference

Even among persistently territorial males the frequency of display is variable (Stirling and Bendell 1966, McNicholl 1978, Niederleitner 1987). However, most published studies of diurnal variation in hooting have been conducted under natural circumstances (Bendell 1955, Stewart 1967, McNicholl 1978), so the patterns reported do not apply to audio-simulated grouse. Stirling and Bendell (1966), for example, found that between the hours of 10:00 and 14:00, when the frequency of hooting among unstimulated males was relatively low, the broadcasting of recorded calls of a female increased the count of hooting males by 110%. Under normal circumstances (without audio stimulation), territorial males cease displaying when they are resting, foraging, or engaged in maintenance activities. When a predator or intruder appears (conspecific or otherwise, including human) a male's response can range from silence to heightened display, depending on the type and magnitude of the threat and past habituation (McNicholl 1983). Some studies suggest males with a lower social status or lower-quality territory display less vigorously (without audio stimulation, McNicholl 1978, Lewis 1986). My findings show that when recorded cackle calls of a female are broadcast properly at the scale of a group census (1) the average probability of detecting a persistently territorial male increases to 0.71 (range 0.33–1.0), (2) all territorial males can be detected in three or four repetitions of the census, and (3) audio stimulation is equally effective in the morning and afternoon. In the only similar study, Stirling and Bendell (1966) found broadcast of a female's calls sufficiently effective for all territorial males within audible range to be detected in <2 man-days of effort (three repetitions of the census per day).

Failure to detect displaying males is of greatest concern with landscape-scale censuses because they are conducted only once and depend on audibility beyond 300 m. However, because the objective of landscape-scale censuses is to detect groups of countersinging males rather than individuals, success is achieved by detection of even a single member of a group. If the probability of detecting a single male at the scale of the group is 0.71, the probability of detecting at least one male in a group of audio-stimulated males must also be very high, even though detection distances are greater and sound propagation is less consistent. Furthermore, because landscape-scale transects are spaced ~400–800 m apart, the 1000-m-diameter "audible zone" surrounding each group is traversed by an observer three or four times (Figure 1, × for hypothetical hooting male). To control for attenuating topography, I aligned landscape-scale transects with dominant ridges and spaced them <800 m apart. Two lines of anecdotal evidence from concurrent field work on the Sooty Grouse indicate my landscape-scale censuses were effective. Radiotelemetry technicians who traversed much of the study area during the hooting seasons of 2007–2009 reported no additional hooting sites. Similarly, habitat technicians who searched for fecal droppings in 138 plots of 0.1 ha distributed evenly throughout the study area identified just 4 or 5 sites where the number, diameter, and texture of droppings (Zwickel and Bendell 2004:136) suggested persistent springtime roosting. I visited

each of these areas during the subsequent hooting season and detected no hooting grouse. I believe if any hooting groups went undetected during landscape-scale censuses they were small, comprising only one or two individuals. Males that have few other hooting grouse nearby tend to display less frequently (pers. obs.), presumably because they are less stimulated. Omission of one or two groups of one or two individuals would have had relatively little effect on the total number estimated.

Number and Distribution of Males

The overall density of the Pinecrest Sooty Grouse population, roughly 0.6 male/km^2, is much lower than the 10–30 males/km^2 typically reported elsewhere (primarily British Columbia, Zwickel and Bendell 2004:212). The only published report of a lower density, 0.16 male/km^2, is from a clearcut in coastal Alaska (Doerr et al. 1984). Most areas in which grouse breed at Pinecrest are in unharvested or selectively harvested forest (Bland and Gardner 2013). The only previous California estimate is 2 males/km^2, from the coastal northwest (*D. f. fuliginosus*, Zwickel and Bendell 2004). Bendell and Zwickel (1984) attributed the relatively low densities of southern populations to lower interspersion of forbs, shrubs, grasses, and coniferous and broad-leaved trees. At Pinecrest these components of vegetation are well interspersed, but at a smaller patch scale (Franklin et al. 2002) than in clearcut forests or mosaics of habitats farther north, where most studies of the Sooty Grouse have taken place.

The distribution of males' territories at Pinecrest is more clumped (aggregated) than reported elsewhere. An *R* value of 0.42 indicates the average distance between nearest neighbors is 42% of what would be expected if territories were randomly distributed across the study area. In two previous studies (both on Vancouver Island), territory spacing was found to be uniform (*R* = 1.32–1.98; Bendell and Elliott 1967, Lewis and Zwickel 1981) or random (*R* = 0.99–1.28; Bendell and Elliott 1967). However, the areas covered in these studies were only 0.1–2.9% the size of my Pinecrest study area. When I assessed the distribution of territories at Pinecrest at the scale of the smaller plots used in these studies, it also appeared to be random (or indeterminable because a plot encompassed only a single territory). Lewis (1985a) argued that clumped distribution results from a patchy distribution of the components of high-quality habitat, rather than breeding behavior representing an exploded lek, as suggested by McNicholl (1978). At Pinecrest, males' territories are typically associated with openings in a more or less continuous forest canopy (Bland and Gardner 2013), and a spatially explicit habitat model indicates suitable habitat for breeding males is widespread, yet much is unoccupied (Bland and Gardner 2013).

Uncensused Population Components

My census methods estimate the number of persistently territorial males, not the total grouse population. Females, nondisplaying adult males, and yearling males cannot be censused reliably by visual or auditory means (Zwickel 1982). On the basis of banding studies or hunters' harvest, females typically constitute ~47–53% of the population under normal circumstances

(Zwickel and Bendell 2004). In coastal British Columbia, Bendell and Elliott (1967) and Redfield (1975) reported that ~11–36% of the males are year-lings, with the proportion highest in areas where the population is sparse or increasing. Under normal circumstances, about 4% of yearling males display (Zwickel and Bendell 2004). A few nonterritorial, nondisplaying adult males have also been identified in intensively studied populations, but their relative abundance remains poorly known (Bendell and Elliott 1967, Lewis 1984).

Management Implications

The census method I have developed is an effective and relatively efficient means of monitoring Sooty Grouse populations, applicable to assessing the effects of development and forest management at a local scale. Monitoring at a regional scale, however, requires less labor-intensive methods. The method most widely advocated for regional population monitoring is sampling by point counts (Ralph et al. 1995), which has been widely adopted for multispecies monitoring (Manley et al. 2004). Point counts, however, were designed primarily for passerines, and are not well suited for the Sooty Grouse. Ideally, the findings of this study would be used to develop a regional monitoring program specifically for the Sooty Grouse. Alternatively, they could be used to design supplemental procedures for existing multispecies point-count programs, thereby improving their effectiveness for tracking Sooty Grouse populations.

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Female Mount Pinos Sooty Grouse (*Dendragapus fuliginosus howardi*), Giant Sequoia National Monument, California, 31 May 1992.

Photo by James D. Bland