# SUGGESTED STUDY ATTRIBUTES FOR MAKING USEFUL POPULATION DENSITY ESTIMATES

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*ABSTRACT*: Estimating density has been a frequent objective of wildlife studies. Interpreted as the spatial intensity of the study animal, density often is compared intra- and inter-specifically for developing ecological theory, assessing human impacts, and setting harvest quotas and instigating abatement programs. However, density estimates seem to be scale-dependent, varying more with the size of the study area than with the corresponding abundance. I therefore suggest that density estimates would be made more useful to theory and policy decisions by specifying that each estimate was made from a study area encompassing all of a population or metapopulation. I also suggest that density estimates would be made more useful by more equitably representing species across taxonomic Orders and Families and within each region, and by representing the range of habitat conditions from within the geographic range of each species. Their usefulness would also improve by describing the larger spatial context and historical background of each population comprising each estimate. Thus, in this paper, I list the study attributes that, if reported in the literature along with each density estimate, would: (1) improve the consistency and usefulness of each estimate, (2) reduce the writing time, and (3) improve the clarity of thought put into the study objectives and its design.

*Key Words*: conservation, density, population, sampling, social organization, study design.

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Field biology provides the foundational information for sound ecological theory, wildlife management, and conservation policy. This information is most useful when it is relevant to the problems or issues dealt with by theorists, managers and policy-makers. It is also useful when it is reported in a consistent, comprehensible manner that enables reliable comparison with other reports of the same or related information. Data are more likely to be worth the effort of collecting them when they are relevant and comparable to each other or to a standard.

Population density is a commonly reported attribute of wildlife populations. The number of animals per unit area or per unit length is intended to express the spatial intensity of populations, which enables intra- and inter-specific comparisons of impacts on the environment or of environmental impacts on the species. Density is often used to justify management policies. For example, the US Department of Agriculture's Animal Damage Control program relies on the relationships between coyote (*Canis latrans*) density and livestock depredation rates to rationalize its coyote control program (USDA 1997). Density was also central to assessing the effectiveness of hunting as a management tool for wolves (*Canis lupus*), grizzly bears (Ursus arctos), and black bears (*Ursus americanus*) in Alaska (Ballard et al. 1996, Miller et al. 1996). Finally, responding to repeated petitions to list the Northern Goshawk (*Accipiter gentilis atricapillus*) as Threatened under the Endangered Species Act, Kennedy (1997) compared the available density estimates through time as part of her argument that the petitioners lacked sufficient evidence of a range-wide decline of Goshawks. However, Smallwood (1998) and Kennedy (1998) disagreed over how Kennedy used the collection of Goshawk density estimates published in the literature.

Density also is a key operational term in ecology, and its use in theoretical model-building has escalated over recent decades (Peters 1991). It has become the favorite expression of the species' spatial intensity in the environment, bearing on the storage and flows of embodied energy and nutrients, interactions with other species, and whether many behaviors and demographic factors are density-dependent. A sampling and interpretive framework would improve the use of density as one of the key foundations of wildlife management, conservation policy, and ecological theory.

Density estimates can be highly variable. Smallwood and Schonewald (1996, 1998) explained most of the variation in density estimates among species of mammalian Carnivora by the size of the study area, which was a result repeated for primary mammalian herbivores (Blackburn and Gaston 1996), pocket gophers (Geomyidae; Smallwood & Morrison 1998), Falconiformes (Village 1984, Smallwood 1995), and breeding birds (Verner 1980). This influence of study area size was a surprise, and was not previously dealt with in ecological hypothesis-testing, wildlife biology or conservation biology. Smallwood and Schonewald (1998) could explain only slight variation in density using variables that represented census methods, types of estimators, vegetation descriptions, land uses, and other study attributes. Their comparisons revealed that the published density estimates among Carnivores provided surprisingly little insight into intra- and inter-specific relationships or into population status. Their comparisons revealed that the size of the study area had much more influence on density estimates than did sampling methods, estimators, and representations of habitat. The failure of Smallwood and Schonewald (1998) to explain much of the variation in density with any variable other than study area size might have been due to inconsistencies in reporting methods, rather than a lack of relationship between these variables and density.

Therefore, the purpose of this present paper is to propose study design and reporting attributes that can improve the usefulness of density estimates. Central to my recommended attributes of study design is the idea that animals occur in aggregations across their geographic range, either due to natural causes or to constraints imposed on their distribution by human land uses. This idea that species are aggregated is supported by empirical evidence (e.g., Taylor and Taylor 1979, den Boer 1981, Hanski 1994, Smallwood 1999). Herein, I suggest a format for reporting density estimates, which can save time with report preparation, improve the usefulness of the report, and provide a simple fill-in-the-blanks form for submission of the appropriate data to a comprehensive, centralized data base.

## STUDY SUBJECTS

Density estimates would be more suited for drawing inter-specific generalizations by providing representation of the available species pool within each of the larger taxonomic groups, e.g., Class, Order, Family. Globally, only 31% of the species of mammalian Carnivora have been studied in ways that led to estimates of density or abundance (Smallwood and Schonewald 1998). Rather than repeatedly studying the economically significant or charismatic species, investigators could more effectively contribute to scientific understanding of patterns of animal abundance by studying previously neglected species. For example, wolverine (*Gulo gulo*) are represented by only four density estimates in the literature that I have surveyed, and jaguar (*Panthera uncia*) by none.

Density estimates also would be more suited for drawing inter-specific generalizations by providing consistent representation of habitat conditions, so that densities and habitat can be compared together wherever they are represented across the geographic range. Study sites need to be chosen to maximize coverage of the geographic range, lest results from one part of the range be inappropriately applied to the remainder of the range. This need is especially important for making assessments of range-wide trends in abundance of candidate or listed threatened and endangered species (Smallwood 1998). Linking density estimates to habitat across a species' geographic range could contribute to critical habitat designation, which is an important step in the Endangered Species Act.

## STUDY DESIGN ATTRIBUTES

Most published estimates of population density lack evidence that the estimates were based on all individuals or all adults composing the "population." Odum (1959) and Dasmann (1981) defined the population as some collection of organisms of the same species occupying a particular space and sharing a suite of attributes representing a unique organizational structure. It is difficult in practice, however, to identify an entire population. Smallwood (1999) provided a possible solution to this problem by identifying a spatial scale domain for each of 30 Carnivore species in which a typical, albeit highly variable, abundance occurred. In this manner, he let the density estimates indicate the abundance of the typical population of each species.

Starting with a conventional study design involving a single site and a single study area boundary, there are several ways to extend the spatial reach of a study to more adequately identify the approximate boundary of the population. Multi-scale censuses or sampling would be the ideal approach for identifying population boundaries, although the cost of censuses or sampling methods could multiply by the additional area put under study. The original study area also could be extended by calibrating the sampling methods used in the intensive area with those used along a transect or in subplots located within and beyond the boundary of the original study area. For example, the abundance estimated using capture-recapture methods can be related to track counts, flush distances, sighting distances, camera detections, visits to bait stations, or to the occurrence frequency of markers in scats. These linked sampling methods can then be extended inexpensively well beyond the original study area boundary in line, strip or belt transects, in subplots, or whatever sampling structure is appropriate.

The purpose of multi-scale census, or of extending sampling beyond the study boundary, is to identify the spatial extent to which the density observed in the intensive study area is representative. If the investigator chose the study site based on a priori knowledge of high density, as is typical (Smallwood and Schonewald 1998), and if animal species are typically clustered in the wild, then steep gradients in abundance should inform the field researcher of a likely population boundary. The population boundary should be recognizable by a circumference in which home ranges no longer overlap or abut each other or where sign of a species transitions from abundant to near absent. That these patterns should be apparent was illustrated recently by a state-wide track count for puma (*Puma concolor*) in California. Smallwood (1997) found 84-86% of all track sets within 4-5 clusters that comprised 23-29% of the transect during counts in 1986, 1992, and 1995. Similarly, Schaller et al. (1988) found snow leopards (*Panthera uncia*) to occur in only about 9% of their range within the Himalayas.

Another approach to characterizing the spatial pattern of abundance of a species is to sample large areas in a random or systematic manner. Ideally, study sites should be chosen randomly or systematically from throughout the species' range, or at least across large areas or regions. Smallwood (1997) used such a sampling approach to estimate about 1100 puma in California. In another example, Hall et al. (1997) counted Hawaiian Hawks ('io; *Buteo solitarius*) at 399 locations along 40 transects across the species' range, and estimated that Hawaii supports 1,600 Hawaiian Hawks at a density of 0.004 hawks/ha. Such sampling can reveal a more realistic pattern of abundance. A frequency distribution of abundance (density) categories could then be estimated for each species. Such frequency distributions could offer reliable, useful representations of abundance patterns across large areas. Frequency distributions of abundance can be tested for representation by probability distribution functions, from which region-wide abundance could be predicted. The comparative value of abundance estimates and their predictability would be much improved.

## REPORTING ATTRIBUTES

Regardless of the approach used to extend the scope of conventional field studies, reporting also needs to be improved to make comparisons easier. Smallwood and Schonewald (1998) found shortfalls in reporting methods that likely contributed to their failure to explain much more of the variation in Carnivore density than could be explained by the size of the study area. In the literature they found a reporting structure that was fairly consistent and helpful in some respects, but still varied considerably in detail and quality (i.e., interpretability).

The typical reporting structure of introduction, methods, results, and discussion was most effective in directing the reader to find information in various sections of the study. The most critical sections of the report are the Methods and Results sections. These sections largely determine the usefulness of the study for withdrawing data. However, critical data are often poorly reported in these sections. For example, the size of the study area is often not reported, thereby rendering the density estimates as useless for comparisons between sites or species. The location of the study also is often vaguely reported, lacking any geographical coordinates or study boundary. Complete descriptions of the study site conditions are rare. Environmental conditions bearing on the density estimates include land use practices (e.g., ownership and land use goals, farming and grazing intensities, hunting quotas, timber harvest regimes, mining activities, human densities), topography, hydrology, vegetation, and regional context. Study reports rarely include maps or descriptions of all these site attributes, despite the availability of mapping tools and data base software (e.g., Geographic Information Systems). Descriptions of the abundance of forage, cover, and nest sites also are rarely provided along with the density estimates, making post hoc density comparisons difficult.

Reports of capture studies usually mention in the Methods section that the captured animals were weighed, yet the weights are rarely reported. The body masses of the animals composing the density estimates would be very useful for studies of ecological energetics and life history attributes (e.g., Calder 1984, Peters 1984). Similarly, the Methods often state that age and sex of the captured animals were recorded, but age distributions and sex ratios do not always get reported in the Results.

## CONCLUSIONS

Wildlife biologists have provided an impressive collection of density estimates in the published literature. However, density estimates will be made more useful by implementing some changes in study design and reporting methods.

To extract information from published reports of density, I offer a data sheet that can serve as a guide for prospective authors of reports of density estimates (Appendix I). Authors can cross-check their available data with Appendix I to ensure that all of it is included in their reports. Appendix I might also save some authors time in constructing their reports. Appendix I also can be completed by those investigators who do not choose to publish their research results related to density estimates. Appendix I can be copied, filled out to the extent possible, and sent to me for inclusion in a growing data base that soon will be available to the public for analysis.

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APPENDIX I

Reference (complete):

Purpose of study: ______________________________

Time period spent in the field: ______________________________

Attach geo-referenced map(s) that depicts study area boundary, land holdings, land uses, vegetation complexes, physical relief, hydrology, approximate locations of study animals, their home ranges, or use areas. If not possible to provide all or some of these maps, then prove the following information.

Name of study site or nearest landmarks: ______________________________

Latitude and Longitude ______________________________

Elevation (meters): Low _______ High _______ Middle or average value _______

Vegetation description:

Topographic relief:

Hydrology:

Name of title-holder(s) or manager(s) of the land:

| Land use | Describe rates or intensities | Types, species, or method |
|---|---|---|
| Timber harvest | | |
| Livestock grazing | | |
| Hunting | | |
| Mining | | |
| Recreation | | |

| Record number | Species | Year | Season or month | Study area (give units) | Abundance or density[1] | Type of Density [2] |
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[1] Circle the appropriate estimate.
[2] Types of density: 0 = 'crude' or total area that is encompassed by the boundaries of the study site; 1 = ecological or habitat area remaining after the species' unused portions of the study area are subtracted from the total area; 2 = Total Area Method, where overlapping territories were subtracted from the occupied area; 3 = home range, pack territory, or cluster of home ranges, or combination of ecological and home range density; 4 = linear, such as along a coast line or river.

| Record number | Census Method (citation) | Estimator (citation) | Reliability or confidence in estimate |
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| Record number | Number captured | Number killed accidentally | Adult sex ratio | Ratio of adults to juveniles | Number of social groups | Mean group size | Population status or trend |
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| Record number | Female body mass (state units) | | | | | Male body mass (state units) | | | | |
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| Record number | Female home range (state units)[1] | | | | | Male home ranges (state units)[1] | | | | |
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| | Mean | SD | n | Low | High | Mean | SD | n | Low | High |
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[1] Provide the home range estimator and its citation(s): ______________________________
Home range overlap would be useful to report as well.

**Explanation to Appendix I**

Reference: Name of authors or principal investigators, year, title, publication or unpublished data.

Vegetation, Physical Relief, Hydrology, and Land Ownership would be most useful when described with more detail and when the types are presented as percentages of the study area.

Record number: Any sequence of numbers or letters that I can use to link the tables by individual estimates of abundance or density.

Reliability or confidence in estimates can be expressed quantitatively (e.g., SD, SE, CV) or qualitatively (e.g., minimum, conservative, too high, accurate, exact).