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ESTIMATION OF OCELOT DENSITY IN THE PANTANAL USING CAPTURE–RECAPTURE ANALYSIS OF CAMERA-TRAPPING DATA

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Neotropical felids such as the ocelot (*Leopardus pardalis*) are secretive, and it is difficult to estimate their populations using conventional methods such as radiotelemetry or sign surveys. We show that recognition of individual ocelots from camera-trapping photographs is possible, and we use camera-trapping results combined with closed population capture–recapture models to estimate density of ocelots in the Brazilian Pantanal. We estimated the area from which animals were camera trapped at 17.71 km^2. A model with constant capture probability yielded an estimate of 10 independent ocelots in our study area, which translates to a density of 2.82 independent individuals for every 5 km^2 (*SE* 1.00).

Key words: camera-trapping, capture–recapture density estimates, individual recognition, *Leopardus pardalis*, ocelot, the Pantanal

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Neotropical felids, such as the ocelot (*Leopardus pardalis*), are secretive and difficult to study in the field. Estimates of population size are especially challenging. Estimates based on track observations are failure prone and unreliable (Karanth 1995, 1999). Radiotelemetry is constrained by the small number of animals that can be tagged simultaneously, the uncertainty about how many individuals are not tagged, and the high costs and efforts involved (Karanth 1995, 1999).

Recently, automatic camera trapping in combination with capture–recapture statistical modeling has been used to estimate population sizes of wild carnivores. Tiger (*Panthera tigris*) populations have been studied successfully using the natural variation in fur patterns between individual tigers (Franklin et al. 1999; Karanth 1995; Karanth and Nichols 1998). Martorello et al. (2001) captured and marked black bears (*Ursus americanus*) and used subsequent phototrapping data to estimate population size.

Karanth (1995) suggested that using natural variation in fur markings also had potential applicability for other secretive mammals with distinctive markings. In this study, we use this technique to estimate density of ocelots in the Brazilian Pantanal. A few studies have estimated density of ocelots based on radiotracking data (Emmons 1988; Ludlow and Sunquist 1987). Our study is the first published attempt to use camera-trapping data and capture–recapture methodology to estimate population size of felids in South America.

Except for the jaguar (*Panthera onca*), the ocelot is the largest spotted cat of South America. Ocelots are generally solitary, nocturnal, and crepuscular with some diurnal activity, feed on a variety of vertebrates, mainly smaller mammals, and inhabit a range of habitat types (Emmons and Feer 1997; Murray and Gardner 1997). In the Pantanal study area, camera trapping re-

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vealed that ocelots were common, and they were recorded in all nonflooded terrestrial habitats. Three females radiotracked in the southern Pantanal relatively close to our study area had a minimum home range of 0.8–1.6 km^2 (Crawshaw and Quigley 1989). Emmons (1988) found that in Peruvian Amazon rainforest, radiotracked ocelots most often chose different pathways on sequential nights and that they visited the entire home range boundaries every 2–4 days.

MATERIALS AND METHODS

The study was conducted in the upper Rio Negro basin of the southeastern part of the Pantanal floodplain, Mato Grosso do Sul, SW Brazil. The study site is a research and conservation reserve of Universidade para o Desenvolvimento do Estado e da Região do Pantanal (UNIDERP) and adjacent areas (headquarters at GPS position 19°30.403′S; 55°36.791′W). The area consisted of a mosaic of open and closed, and wet and dry habitat types including gallery forest, semideciduous forest islands with the understory dominated by the palm *Schealea phalerata*, dry woodland and savanna, seasonally flooded grassland, and marshes. The habitats of the Pantanal are described in more detail in Prance and Schaller (1982) and Ratter et al. (1988).

Ocelot camera-trapping data were obtained during a general 3-month mammal survey, May–July 2001. We used 6 infrared trail monitors (Trailmasters: 5 passive monitors, model TM550, and 1 active monitor, model TM1550—Goodson and Associates, Inc., Lenexa, Kansas) with camera kits (Trailmaster model TM35-1) using adapted, automatic, weatherproof, 35-mm Yashica cameras with automatic flash. The active system uses an infrared beam between a transmitter and a receiver and is triggered when the beam is broken. The passive system consists only of a transmitter that monitors a wedge-shaped infrared field and is triggered by warm-blooded animals moving through the wedge. On the passive TM550 monitors, we covered the infrared sensor with tape, leaving only a 1-cm vertical gap in the center (assuring that animals would be in the center of the photograph when triggering the trap). We used the following sensitivity settings: P = 2 and Pt = 2. (The infrared wedge is divided into a number of ‘‘windows.’’ P is the number of windows that must be broken by a warm-blooded animal for the trap to be triggered. Pt is the number of seconds allowed for the animal to break these windows.) The advantages of the passive system are that it is cheaper than the active system and is easier to set up. The disadvantages are that in an open, tropical area like the Pantanal, the trap may be triggered by shadows of branches moving in the wind in front of the sensor and that it is difficult for the infrared sensor to ‘‘see’’ warm-blooded animals when environmental temperature is high. To avoid these problems, we programmed units to work only from 1700–0700 h, which we assumed to be the primary period of activity of ocelots. The advantages of the active system are that even in an open area like the Pantanal, it can work both day and night and one can easily choose the minimum size of animals one wants to monitor by setting the height above the ground of the infrared beam. Trailmonitors were set at a height of approximately 20 cm so that ocelots passing the trap stations would always be recorded. Camera delay (the minimum time between 2 photographs) was set at a short period (0.5 min) which, combined with bait, gave a better chance of getting photographs of both flanks of individual ocelots during one capture. We placed stations in all nonflooded habitats at sites such as trails and corridors that appeared to be natural travel routes for ocelots. Sardines in oil were used as bait.

To identify individual ocelots from the camera-trapping photographs obtained, we used a combination of distinguishing characters including the patterns of rosettes, spots and stripes on flanks, sex, length and banding pattern of tails, ‘‘hanging’’ bellies of lactating females, slim bodies of young individuals, and notched ears (Figs. 1 and 2). Males were identified by the presence of testes.

Statistical methods.—We divided our camera-trapping data into twelve 1-week periods, each constituting a ‘‘trapping occasion.’’ This gave a capture history for each ocelot consisting of a string of ones and zeroes indicating whether the individual was camera trapped (1) or not (0) during each 1-week period (see Table 1). To estimate abundance, we used the program CAPTURE (obtainable at www.cnr.colostate.edu/~gwhite/software.html as of 30 April 2002) to implement capture–recapture models for closed populations (Otis et al. 1978). Closed-population models assume that a population remains un-

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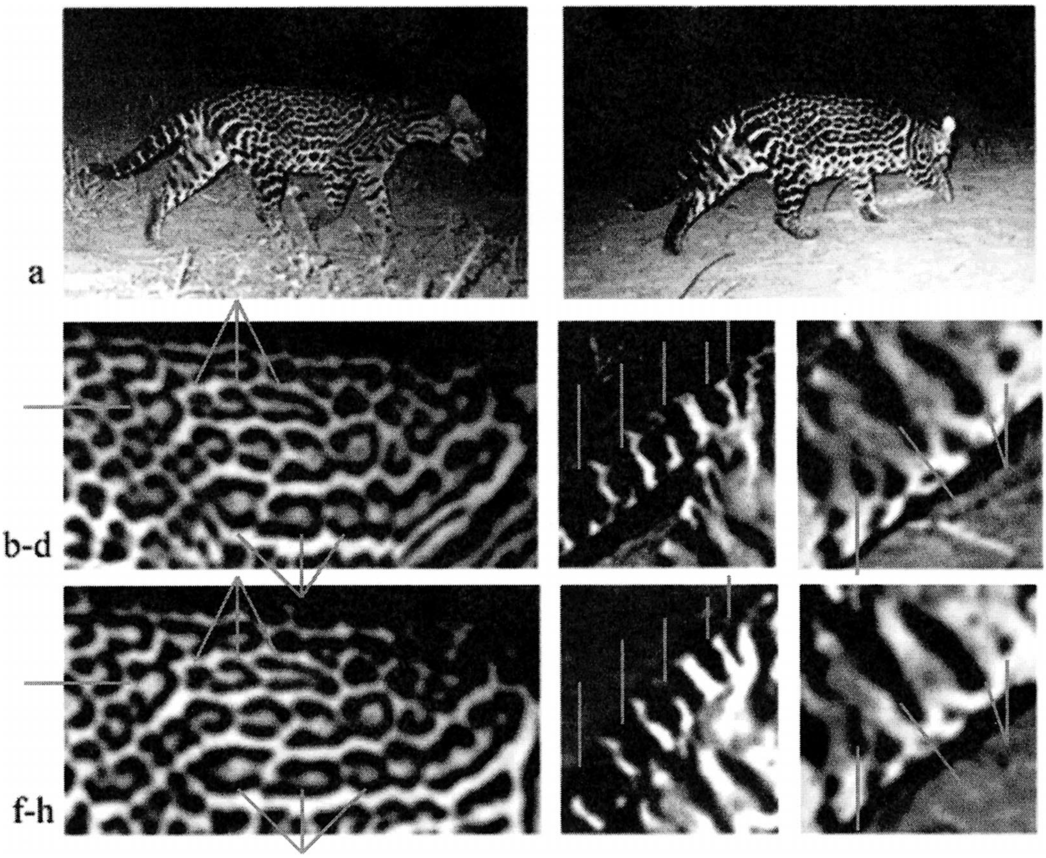

FIG. 1.—Features allowing recognition of individual ocelots, as shown by 2 camera-trapping photographs of the same male at different sites and in different postures, with enlargements of details from flank, tail, and inner thigh. a) Lateral view. b–d) Details from photograph (a). e) Lateroposterior view of same male. f–h) Details from photograph (e). Arrows indicate specific distinguishing fur markings (see text).

changed during the study period, i.e., that there are no gains or losses of individual ocelots (the closure assumption).

We checked the closure assumption (the assumption that our ocelot population did not change significantly during the study period) in 2 ways. First, we applied the closure test implemented in CAPTURE. Because this test is known to have low power and to be sensitive to trap response (G. C. White et al., in litt.), we also applied an alternative procedure. We used program MARK (White and Burnham 1999) to test the open-population Cormack–Jolly–Seber model against a constrained model in which apparent survival was fixed at 1. The latter model again represents a closed-population model, so a comparison between these 2 models tests whether the closed-population assumption is reasonable for this data set (Stanley and Burnham 1999).

Program CAPTURE estimates abundance under 7 models that differ in their assumptions about capture probability. The simplest model, M_0, assumes a constant capture probability across all occasions and animals. Model M_t (where t is time) assumes that capture probability varies between occasions, e.g., due to changing weather conditions. Model M_b (behavior) allows trap response, i.e., capture probability may be different between the 1st capture and all subsequent recaptures of an animal. For example, baiting traps might have caused ocelots to return more quickly to a trap site than they would otherwise have done. Model M_h (heterogeneity) as-

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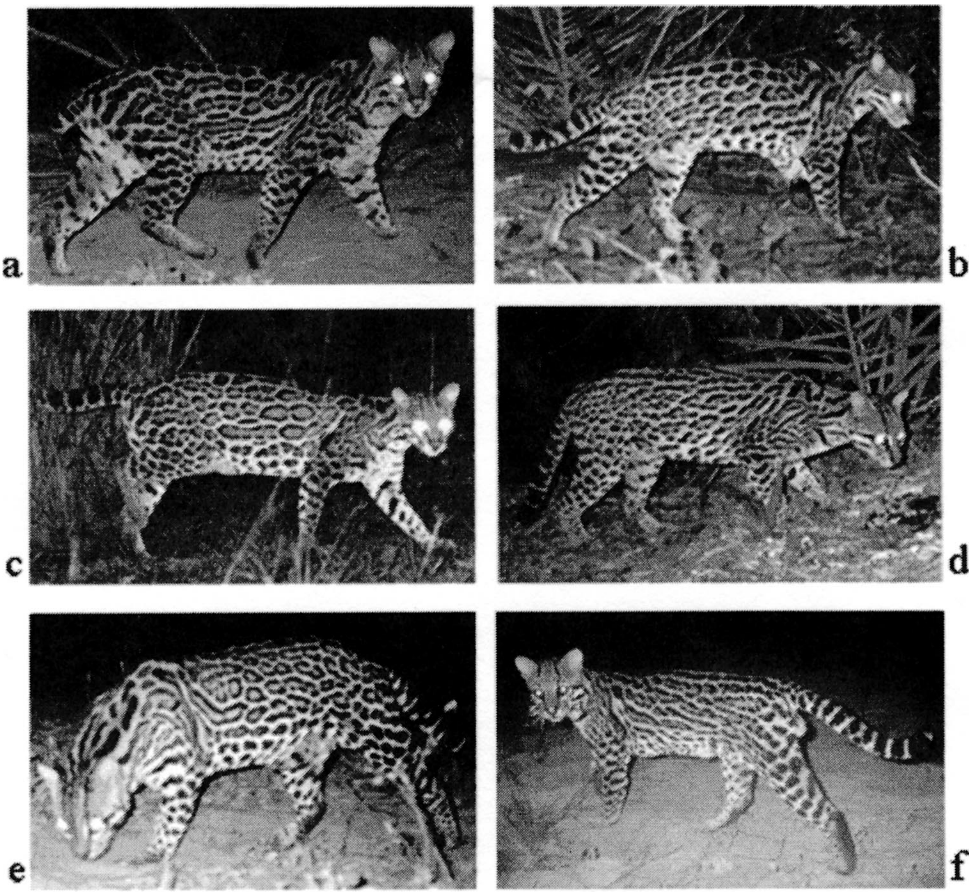

FIG. 2.—Camera-trapping photographs of 6 ocelots, indicating characters used in distinguishing individuals. a) Female (note lack of testes), very short tail, notches in both ears, long series of rosettes melted together; b) female, slender body, medium long tail, isolated medium-sized rosettes; c) lactating female (note hanging belly), short tail, large, round rosettes on upper flank; d) female, long tail, weakly defined rosettes and many small spots and lines; e) male (more strongly built than females), long tail, long rosette on shoulder, additional rosettes on flank circular; f) male (note testes), very long tail, long narrow rosettes.

sumes that each animal had its own probability of being captured, e.g., that individuals with larger home ranges are exposed to more traps. In addition, CAPTURE allows estimation under 3 models that are pairwise combinations of these sources of variation in capture probability (models M_{th}, M_{bh}, and M_{tb}).

To identify an adequate model for estimation, we used goodness-of-fit tests, between model tests, and the model selection algorithm provided in program CAPTURE. We report estimates from program CAPTURE of capture probability, population size, and the standard error of population size based on the most adequate model.

To convert the estimate of population size into an estimate of density, we followed the procedure adopted by Karanth and Nichols (1998). We first calculated a core area as the minimum convex polygon defined by all trapping stations. This core area was unlikely to contain the entire home range of all trapped ocelots. Instead, it is likely that some ocelots had home ranges that extended beyond the core area. To account for that, we added a boundary strip to obtain the total area from which our animals were taken. Strip width was given by half the mean maximum distance moved by ocelots caught on more than 1 trap. This ad hoc approach has little the-

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TABLE 1.—Summary of camera-trapping results. The capture history consists of 12 capture occasions (i.e., twelve 1-week periods). A '1' indicates that an individual was camera-trapped during a particular 1-week period and '0' that it was not. Maximum distance moved is given for individuals camera-trapped at more than 1 site.

Individual	Capture history	Maximum distance moved (km)
Adult females		
f1	000100001000	2.4
f2	000111000010	1.3
f3	000000011000	0.3
f4	000010000110	1.0
Adult males		
m1	000110000100	2.1
m2	010000000000	—
m3	000000010000	0.3
m4	000000000001	—
Subadults		
s1	101000000000	1.1

oretical justification, but it appeared to work well in simulation studies of Wilson and Anderson (1985), and it was the only available means of estimating boundary strip width in our situation. Density was then obtained by dividing the population size estimate by the estimated total area. Formulas for these estimators and their variances can be found in Karanth and Nichols (1998).

RESULTS

During the study period, 30 trapping stations were camera trapped successfully, covering a minimal convex polygon area of 9.26 km^2 fairly regularly. The total camera-trapping effort was about 450 camera-trapping nights. Both the active and the passive Trailmaster systems worked well for ocelots. Sardines in oil proved to be quite attractive to ocelots, as evidenced by many photographs of animals sniffing or eating the bait. Fifty-five camera-trapping photographs of ocelots were obtained on 29 captures and from 13 sites. (We defined a capture as a record of 1 individual. Because of the bait, the ocelots sometimes remained in front of a camera trap long enough for more than 1 photograph to be taken during the same capture. A trapping occasion was composed of a 1-week period. During some 1-week periods, more than 1 capture was obtained of an individual.)

Recognition of individual ocelots.—Many distinguishing characters can be found in the markings of ocelots. Fig. 1 shows an example of 16 characters allowing positive identification of a male ocelot photographed at 2 different sites and in two different body postures. The series of rosettes on the middle and upper flanks and upper shoulder (often in combination with short lines or dots, or both) are generally the best features allowing certain identification of individuals. The pattern seen on the lower part of the shoulder varies greatly according to the position of the front leg. Frequently, long rosettes followed by a specific pattern of smaller rosettes and dots are characteristic (Fig. 1). Tail length, number of bands, and banding pattern (e.g., the specific combination of thin, thick, and broken bands) are often helpful characters. The pattern of large stripes and smaller dots on the inner thigh may also be helpful features. Fig. 2 shows examples of distinguishing characters of 6 additional individuals.

All but 3 of the 55 photographs were identified. Nine individuals could be distinguished: 4 adult males, 4 adult females, and 1 subadult. The capture history for each individual is given as part of Table 1.

Density estimate.—Both closure tests were consistent with the assumption that the ocelot population was closed for the duration of the study (test in CAPTURE: $z = -0.963$, $P = 0.17$; test using MARK: $\chi^2 = 1.384$, $d.f. = 1$, $P = 0.23$). The model selection algorithm in CAPTURE selected model M_0, with constant capture probability, as most appropriate. Its selection criterion was 1.0 compared with 0.81 for the next best model, M_h. Direct hypothesis tests between model M_0 and the competing models M_t, M_b, and M_h gave no reason to reject

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the assumption of a constant capture probability ($P > 0.83$).

The estimated capture probability per occasion and individual was 0.16. The resulting population size estimate was 10 ocelots ($SE = 1.36$) with a 95% confidence interval (CI) of 9 to 14. The estimated probability of catching an ocelot at least once during the entire study period is given by $1 - (1 - 0.1641)^{12} = 0.88$ or alternatively by the ratio of total number of animals caught to estimated population size, $9/10 = 0.90$ (difference due to rounding).

The minimal convex polygon core area of our camera trapping was 9.26 km^2. The total area including the boundary strip of 0.6 km measured 17.71 km^2. The estimated density of ocelots was 2.82 independent individuals per 5 km^2 ($SE = 1.00$; 95% CI = 0.86 to 4.79). The wide CI reflects both a low capture probability (per trapping occasion) and a relatively small trapping area and population size.

DISCUSSION

Biological considerations.—We found a density of ocelots of 2.82/5 km^2 in our Pantanal study area. Only a few attempts have previously been made to estimate ocelot density. Based on radiotelemetry data (home range configurations) and available habitats, Ludlow and Sunquist (1987) estimated density at 1.9 resident ocelots per 5 km^2 in the Venezuelan Llanos. Emmons (1988) estimated density at 4 resident ocelots per 5 km^2 in the Peruvian Amazon.

Methodological considerations.—In the design of a capture–recapture study to estimate density using closed-population models, it is desirable to achieve constant and high capture probabilities and short trapping sessions (of about 1.5–2 months). The former yields unbiased and precise abundance estimates. The latter makes it more probable that the closure assumption is met, which is difficult to test (Kendall 1999). Factors that could affect ocelot capture probability are trap density, duration and definition of the trapping occasion, spatial arrangement of the traps, and trapping details, such as whether baits are used.

Our study had a trap density per trapping occasion of 6/16.3 km^2, corresponding to 1 trap for every 2.7 km^2. We achieved a capture probability per occasion of 0.16. This was probably adequate because a capture probability of 0.1 is usually cited as the lower limit for which meaningful estimates of population size can be obtained (Otis et al. 1978).

In a capture–recapture study, it is essential to appropriately define the trapping occasion. We chose 1-week intervals as our temporal units (occasions). It is important that for each trapping occasion the whole study area is covered well with traps and that there are no ‘‘gaps’’ where individuals are not exposed to any traps at all. Karanth and Nichols (1998) had an alternative study design, which may be more appropriate than ours. They had 4–6 traplines that ran through an entire study area, each trapline with 12–15 camera-trapping points. Their trapping occasion was defined as the 4–6 consecutive nights it took to trap all traplines for 1 night each. An entire trapping session lasted for 9–16 occasions.

In conclusion, we recommend the following. Trapping sessions should be kept relatively short for the closed population assumption to be met. Each trapping occasion may include camera trapping in several (e.g., up to 5) subareas, which allows a larger area to be studied and ensures that the study area is covered equally by camera traps at each capture occasion. The study area should be covered with a trapping-station density that yields a capture probability of at least 0.1. The home range of every target individual within the study area should contain at least a few traps. If economically feasible, 2 cameras should be used on each trapping site so that both flanks of animals are photographed on each capture.

If the same study area is revisited after a longer period (e.g., months or a year), Pollock's robust capture–recapture design can

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be applied, which permits estimation of survival and migration rates in addition to abundance. For a discussion of this useful design, see Kendall et al. (1997) and Williams et al. (2002).

In conclusion, our study successfully applies the use of automatic camera trapping and capture–recapture modeling of the population size, initiated in tiger studies, to another elusive carnivore. We note that, especially at low densities, a host of characters may serve as individual markings, such as sex, length of whiskers, scars, and mutilations (for example, see Fig. 2a). Thus, the use of the techniques used in this study is probably not limited to animals with such strong fur markings as the ocelot or the tiger. Study design, however, deserves sufficient consideration before initiating any study so that as many of the model assumptions as possible are met and that efficient use can be made of the data to model population size and other demographic traits.

RESUMO

A jaguatirica (*Leopardus pardalis*), bem como os outros felinos Neotropicais, são animais discretos e arredios, o que dificulta estimar suas populações utilizando métodos convencionais tais como a rádio-telemetria ou a identificação através de sinais diretos ou indiretos (fezes, pegadas). Demonstramos que é possível o reconhecimento de indivíduos de jaguatirica através do uso de fotografias registradas pelo uso de ‘câmeras-trap’. Utilizamos os resultados obtidos com o uso das ‘câmeras-trap’ combinados com modelos de captura e recapturas para populações fechadas para estimar a densidade populacional das jaguatiricas no Pantanal do Brasil. A área estimada dos animais registrados foi de 17.71 km^2. Um modelo de probabilidade de captura constante produziu uma estimativa de 10 jaguatiricas em nossa área de estudo, o que se traduz para uma densidade de 2.82 indivíduos independentes por 5 km^2 (*SE* 1.00).

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