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ESTIMATES OF ABUNDANCE OF BOX TURTLES (*TERRAPENE CAROLINA BAURI*) ON A FLORIDA ISLAND

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ABSTRACT: From 1991–1993, we conducted an intensive mark-recapture study of an island population of Florida box turtles, *Terrapene carolina bauri*. We used models based on the Jolly-Seber open population model to estimate abundance, after first examining the capture histories for violations of the underlying assumptions of mark-recapture analysis with goodness-of-fit tests contained in the program RELEASE. Some violations were detected, resulting in low estimates. We estimated that 544 (415–672 approximate 95% confidence interval) adult box turtles inhabited the southern 36.4 ha of Egmont Key in the summer of 1993. This estimate is similar to those of conspecific populations studied in more northern areas and provides a reliable initial estimate with which to monitor population trends in the future. Adult capture probabilities ranged between 0.09 and 0.30. Weekly survival probabilities for adults ranged between 0.94 and 1.00. There were significant differences in capture histories between adults and juveniles, indicating differences in survival and/or capture probabilities. Increased movement and activity of individuals on the study area during two survey periods, one after a severe storm and the other during the fruiting season of a favorite food source, was verified with one of the goodness-of-fit tests.

Key words: Box turtle; Island; Florida; Abundance; Population size estimation; Movement patterns; Mark-recapture; Open population models

EASTERN box turtles (*Terrapene carolina*) are often perceived as common. However, long-term studies of the population dynamics of this species have been conducted only in the northern third of its range (Schwartz et al., 1984; Stickel, 1978; Williams and Parker, 1987). Empirical data are lacking for the Florida box turtle (*Terrapene carolina bauri*). Beginning in 1991, we began a mark-recapture project monitoring a population of Florida box turtles that inhabits Egmont Key, an island situated at the entrance to Tampa Bay harbor, Hillsborough County, Florida (Dodd et al., 1994). Although the 180-ha island has a long history of human occupation (Franz et al., 1992), it presently is a National Wildlife Refuge and State Park with limited access to the public.

In addition to possible comparisons with more northern populations, monitoring this particular population is of interest in terms of its population dynamics. The island on which it is found is subject to various natural and human-related influences that can affect population dynamics, including flooding from storms and hurricanes (see Franz et al., 1992, for a review) and habitat management by park personnel (Dodd et al., 1994). A realistic assessment of changes in abundance through time can provide insight concerning the impact that these influences may have on this long-lived species.

Previous long-term studies of box turtles have indicated declines in populations (Schwartz et al., 1984; Stickel, 1978; Williams and Parker, 1987). These studies, however, lacked variance estimates for their estimates of population size. Rigorous statistical methods to detect time trends and to test hypotheses concerning temporal differences in population size require estimates of variance (Link and Nichols, 1994; Skalski and Robson, 1992). Open and

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closed mark-recapture models now provide the statistical methods to estimate population size and variance, but biologists using these methods with many aquatic and terrestrial turtle populations often overlooked the assumptions involved in open and closed population models (reviewed by Lindeman, 1990). Violations of assumptions can seriously bias estimates (Carothers, 1973; Gilbert, 1973).

New mark-recapture statistical models are now available in user-friendly programs that run on personal computers (Nichols, 1992), and goodness-of-fit (GOF) tests have been developed that test for violations of the equal probability of capture assumption that must be met in order to apply the statistical models to the data appropriately. Differences in capture probabilities identified by these same GOF tests also can provide information on behavior patterns. We used these new methods and computer programs to examine our capture data for violations of assumptions and to estimate abundance during 1992 and 1993. Our analysis provided an initial estimate for future comparisons as we continue to monitor the population. We also compared our results with estimates of box turtle numbers in habitats and latitudes different from our study site.

Methods

Capture data used in the analysis were collected on 11 three-day surveys of Egmont Key from March 1991 through July 1993 (see Table 2 below for dates). Because logistical problems prevented us from systematically sampling the entire 180 ha of the island, we restricted our analysis to data collected on the southern part of the island, south of the Cross Island Trail (Fig. 1 in Dodd et al., 1994). The area totaled approximately 36.4 ha. The most extensive habitats were forest composed of cabbage palm (*Sabal palmetto*), Australian pine (*Casuarina equisetifolia*), and Brazilian pepper (*Schinus terebinthifolius*), and mowed lawn at the compound of the Tampa Bay Pilot's Association.

Turtles were captured by hand and classified according to sex and adult or juvenile status. Juveniles were <10 cm carapace length and could not be identified to sex. Each individual was marked with a pattern of unique shell notches for future identification (Cagle, 1939) and released. We compiled capture histories by recording the presence or absence of individuals during each of the 11 survey periods. Additional descriptions of the habitat and field methodology are contained in Dodd et al. (1994).

The choice of a statistical approach to estimate abundance from mark-recapture data depends on whether the population is closed or open to birth/immigration and death/emigration. A population may be considered closed if the sampling period is short in duration such that birth and death or immigration and emigration are non-existent. If data are collected over weeks or months, individuals entering or leaving the population confound the analysis and open population models must be used. Closed population models permit relaxation of the assumption of equal capture probabilities, and hence they provide more robust estimates of population size than open models when this assumption is not met (Pollock, 1982). However, logistical constraints prevented us from making extended trips to the island to collect capture data under a closed design. We therefore used the open population approach.

Before applying open models to the data, we assessed how well the capture histories met the following assumptions necessary for mark-recapture analyses. (1) Every marked individual present in the population immediately after the ith sample has the same probability of survival (ϕ_i) until the following sample ($i + 1$). (2) Every individual in the population at the time of the ith sample has the same probability of capture (p_i). (3) Marks are not lost or overlooked. (4) All samples are instantaneous and each release is made immediately after the sample.

Assumption 3 was not a problem in this study, because the shell notches provided a permanent and unambiguous mark. In four years, we never observed any wear around the notches that would cause them to be misread. Assumption 4 was also met by our methods. Because each survey was restricted to three days, the sampling interval was short enough not to be affected by death/emigration or birth/immigration. We ascertained the validity of assumptions 1 and 2 with several GOF tests in program RELEASE (Burnham et al., 1987).

We examined the equal probability of capture and survival assumptions by grouping individuals a priori according to categories that one might consider as being subject to different mortality regimes or activity patterns and then testing for differences in capture histories among groups with TEST1 of program RELEASE. The three groups that we considered were adult males, adult females, and juveniles. We specifically examined the equal probability of capture assumption for each group and for all groups combined using TEST2 and TEST3. TEST2 detects differences in capture probability within individual capture histories due to a response to being captured (i.e., "trap happiness" or "trap shyness": Pradel, 1993). TEST3 detects differences in capture probability among individuals due to previous capture history (the most common case being the presence of transients, individuals caught only once and then never recaptured: Burnham et al., 1987; Paradis et al., 1993).

We estimated population size, capture probabilities, and survival probabilities for each survey period with program JOLLY (Pollock et al., 1990). Three variations of the classic Jolly-Seber open population model were compared for suitability to the data for box turtles: Model A, the general Jolly-Seber model which allows capture (p) and survival (ϕ) probabilities to vary over the survey periods (i) (ϕ_i, p_i, in the notation of Lebreton et al., 1992); Model B, which assumes that survival probabilities are constant over the study period while capture probabilities vary (ϕ, p_i); and Model D, which assumes both the survival and capture probabilities are constant during the study period (ϕ, p). The best fitting model for estimating the parameters was chosen based on likelihood ratio tests between models.

Results

We captured and marked 718 box turtles during the study. There were 365 males, 248 females, 102 juveniles, and three adults of unknown sex.

Tests for Violations of Assumptions

Some violations of the assumptions of equal probability of capture and survival were indicated. TEST1 of RELEASE showed no significant differences in capture histories between adult males and females ($\chi^2 = 19.45$, 19 df, $P = 0.428$). However, significant differences were detected ($\chi^2 = 93.23$, 34 df, $P < 0.0001$) between adults and juveniles. The results of TEST2 for all groups pooled indicated no effects due to any behavioral response to capture and handling ($\chi^2 = 26.20$, 34 df, $P = 0.83$). TEST3, however, showed evidence of an overall deviation from the assumption ($\chi^2 = 53.38$, 36 df, $P = 0.03$). Examination of the two component tests of TEST3, TEST 3.SR and TEST 3.Sm, showed that only TEST 3.SR was significant. This test indicates an effect due to transients in the study area that were captured once and never recaptured. Further examination of TEST 3.SR for each survey period showed that the effect occurred only during two of the surveys. The two violations occurred during survey 7 in October 1992 ($\chi^2 = 5.48$, 1 df, $P = 0.019$) when individuals were found aggregating beneath fruiting vegetation, and during survey 8 in April 1993 ($\chi^2 = 11.32$, 1 df, $P = 0.0008$) 1 mo after a severe storm destroyed vegetation on parts of the island (Dodd et al., 1994). TEST2 and TEST3 pooled, which tests for goodness-of-fit to the general Jolly-Seber model (Lebreton et al., 1992), was not significant ($\chi^2 = 79.09$, 70 df, $P = 0.22$).

When we examined males, females, and juveniles separately for homogeneity in capture probabilities, similar results were found (Table 1). Neither TEST2 nor TEST3 overall was significant for any group. TEST 3.SR indicated an effect from transients for males only. Examination of the test for each survey period showed that transients had a significant effect during survey 8, just after the storm of March 1993 (χ^2 = 11.44, 1 df, P = 0.0007). Although TEST 3.SR overall was not significant for females, the test for each survey period indicated a significant effect from transients during survey 7 when turtles were observed aggregating under fruiting vegetation (χ^2 = 6.90, 1 df, P = 0.0086). Up to 30 individuals were found under one sea grape bush during this period (Dodd et al., 1994). These same patterns were identified in the tests of the combined data.

The results of the GOF tests for adults only indicated that males and females were homogeneous in capture and survival probabilities and supported the pooling of data to estimate adult abundance on the southern portion of Egmont Key. The pooled data fit the Jolly-Seber model well (TEST2 and TEST3 pooled χ^2 = 108.16, 100 df, P = 0.2739).

The results of the GOF tests did not support pooling capture histories of adults and juveniles. However, sample sizes were too small to consider juveniles in a separate analysis, and estimates based on two age class models, such as those available in program JOLLYAGE (Pollock et al., 1990), were not possible because the transition from juvenile to adult status may occur over a range of sizes and, therefore, ages. Nonetheless, because no previous study had included juveniles in an estimate of population size for box turtles, we elected to include a pooled analysis, realizing that our estimates were biased.

TABLE 1.—Summary of goodness-of-fit tests of data to the assumption of equal probability of capture among individuals within a survey period using program RELEASE. Data grouped according to adult males, adult females, and juveniles.

Group	Test	χ^2	df	P
Males	TEST 2	31.26	29	0.35
	TEST 3.SR	17.49	9	0.04*
	TEST 3.Sm	19.68	21	0.54
	TEST 3	37.16	30	0.17
	TEST 2 + TEST 3	68.43	59	0.19
Females	TEST 2	14.18	20	0.82
	TEST 3.SR	14.00	9	0.12
	TEST 3.Sm	11.55	12	0.48
	TEST 3	25.55	21	0.22
	TEST 2 + TEST 3	39.73	41	0.53
Juveniles	TEST 2	2.18	7	0.95
	TEST 3.SR	6.54	6	0.37
	TEST 3.Sm	4.67	3	0.20
	TEST 3	11.21	9	0.26
	TEST 2 + TEST 3	13.39	16	0.64

* Significant at α = 0.05.

Estimates of Parameters

For the analysis that included adults only, Model A (the general Jolly-Seber model with variable survival and capture probabilities) was indicated as the best model. Capture probabilities estimated for each survey ranged from 9.6–30.5% with the lowest estimates occurring at the beginning of the study, when a small proportion of the population was marked (Table 2). By the fifth survey, capture probabilities increased to >20% (range 20.5–30.5%). Only during the eighth survey after a storm had damaged portions of the island's vegetation did the capture probability fall to earlier levels. Estimates of weekly survival based on the adult capture histories were high (Table 3).

Estimates of population size over the study ranged from 422–645 adults (Table 4). However for survey 2 through 4, the coefficients of variation (CV) were high relative to those of estimates calculated later in the study when a larger number of individuals was marked. A higher proportion of marked individuals in the population leads to more reliable estimates (Pollock et al., 1990). Estimates for surveys 7 and 8 were higher than those of surveys 5, 6, 9, and 10, but the high estimates were for the two surveys when the GOF tests indicated an effect from transients. The best initial estimates for future comparisons are most likely from surveys 9 and 10 at 544 (95% CI 415–672) and 531 (95% CI 392–669) adults.

For the analysis that pooled adults and juveniles, Model B (constant survival probabilities and variable capture probabilities) was indicated as the best model. Capture probabilities estimated for each period were lower than for adults only and ranged from 7.3–26.5% over the study period. The estimates of abundance were similar for the last three survey periods and ranged

TABLE 2.—Probability of capture of an individual for each survey period estimated under Model A (ϕ_i, p_i) of Program JOLLY; n = total number of individuals captured. Capture histories included adults only.

Period	Date	n	Probability of capture	$\hat{SE}$	95% confidence interval
2	23–25 April 1991	73	0.096	0.042	0.013–0.178
3	22–23 Jan. 1992	59	0.134	0.034	0.067–0.201
4	20–22 Feb. 1992	54	0.114	0.030	0.056–0.172
5	21–23 April 1992	156	0.305	0.041	0.224–0.385
6	19–21 June 1992	142	0.251	0.033	0.187–0.314
7	16–18 Oct. 1992	131	0.210	0.029	0.154–0.266
8	23–25 April 1993	80	0.127	0.022	0.084–0.171
9	17–19 May 1993	112	0.205	0.030	0.147–0.263
10	16–18 June 1993	143	0.269	0.041	0.190–0.347

from 582–630 individuals (Table 5). Pooling capture histories for adults and juveniles violated the assumption of equal probability of capture and survival, and the calculated confidence intervals do not reflect the uncertainty introduced by the violation.

DISCUSSION

Our data on the box turtle population at Egmont Key met the assumptions of the mark-recapture models for open populations fairly well. Tests detected only two violations of the assumptions of equal probability of capture and survival; there were significant differences between adults and juveniles in capture histories, and there was an influx of transients that were caught in two survey periods and then were never recaptured. Identifying these violations, however, does not negate the analysis but gives a better picture of the reliability of our estimates, and we have interpreted results and drawn inferences accordingly.

The degree of bias in our estimates introduced by the presence of transients depends on the source of the transients. If the transients are from areas outside of our study site, they do not represent a severe violation of the assumption of equal probability of capture, as the effect was confined to only two of the survey periods. If the transients, however, are undetected residents that were captured only when they changed their behavior in response to the storm or the appearance of the fruit, it draws into question the assumption of equal probability of capture between marked and unmarked individuals. Persistent differences between marked and unmarked residents in average capture probabilities will result in an over-estimation of the true proportion of marked animals in the population and an under-estimation of abundance (Pollock et al.,

TABLE 3.—Estimates of weekly survival probabilities between survey period i to $i + 1$, calculated under Model A (ϕ_i, p_i) of program JOLLY.

Period	Date	Survival probability	$\hat{SE}$	95% confidence interval
2	23–25 April 1991	0.970	0.023	0.924–1.000
3	22–23 Jan. 1992	1.000	0.003	0.995–1.000
4	20–22 Feb. 1992	0.937	0.033	0.872–1.000
5	21–23 April 1992	0.992	0.012	0.969–1.000
6	19–21 June 1992	0.988	0.010	0.969–1.000
7	16–18 Oct. 1992	0.996	0.006	0.985–1.000
8	23–25 April 1993	0.998	0.005	0.989–1.000
9	17–19 May 1993	0.977	0.046	0.887–1.000
10	16–18 June 1993	0.973	0.039	0.897–1.000

TABLE 4.—Estimates of population size ($\hat{n}$), standard error (SE($\hat{n}$)), coefficient of variation (CV), and approximate 95% confidence intervals (95% CI) for adults only under Model A (ϕ_i, p_i) of Program JOLLY.

Period	Date	$\hat{n}$	SE($\hat{n}$)	CV	95% CI
2	23–25 April 1991	646	271	0.42	113–1178
3	22–23 Jan. 1992	422	94	0.22	237–608
4	20–22 Feb. 1992	454	103	0.23	253–655
5	21–23 April 1992	505	60	0.12	387–623
6	19–21 June 1992	562	61	0.11	441–682
7	16–18 Oct. 1992	618	67	0.11	482–755
8	23–25 April 1993	623	89	0.14	449–796
9	17–19 May 1993	544	65	0.12	415–672
10	16–18 June 1993	531	71	0.13	392–669
11	cannot be estimated under Model A				

TABLE 5.—Estimates of population size ($\hat{n}$), standard error (SE ($\hat{n}$)), coefficient of variation (CV), and approximate 95% confidence intervals (95% CI) including adults and juveniles under Model B (ϕ, p_i) of Program JOLLY; n = total number of individuals captured. Due to violations of the assumption of equal probability of capture and survival, SE (n), CV, and 95% CI do not accurately reflect the uncertainty of the estimates.

Period	Date	n	$\hat{n}$	SE ($\hat{n}$)	CV	95% CI
2	23–25 April 1991	87	1190	484	0.41	242–2138
3	22–23 Jan. 1992	67	442	72	0.16	301–583
4	20–22 Feb. 1992	68	642	113	0.18	420–864
5	21–23 April 1992	188	699	64	0.09	574–825
6	19–21 June 1992	155	758	56	0.07	648–867
7	16–18 Oct. 1992	137	747	51	0.07	648–846
8	23–25 April 1993	85	672	54	0.08	566–778
9	17–19 May 1993	120	582	34	0.06	515–649
10	16–18 June 1993	151	630	36	0.06	559–700
11	27–29 July 1993	157	598	30	0.05	539–657

1990). We do not know the source of the transients at period 7 and 8. During other surveys, we observed individuals moving both north and south of the Cross Island Trail that marked the northern limits of our study site; migration from the mainland, however, is highly improbable. Undetected residents, however, also could have contributed to the appearance of transients making our estimates of adult abundance lower than the true value.

Abundance estimates for adults and juveniles are definitely biased due to the differences in capture histories between the two groups. Given our perceptions of abundance and the characteristics of the environment (e.g., large prey base, lack of mammalian predators, lack of recent human disturbance), however, we believe these estimates to be within reason.

Comparing our estimates with those from other studies at different localities is problematic. Bias and precision of the estimates in the other studies are unknown, because violations of assumptions were not examined or estimates of variance were not calculated. Furthermore, in order to facilitate comparisons within a common framework, previous estimates were presented in many of the studies as density/ha or density/acre, which introduces additional problems. Density may be overestimated if an "edge effect" is not considered. Animals on the boundary of the study area often do not have their entire home range within the study area, and inclusion of these individuals can introduce bias. Only recently has the problem been approached in a rigorous statistical framework (e.g., Otis et al., 1978), although some earlier authors (e.g., Stickel, 1950) were aware of the problem. Bias also can be introduced if it is assumed that habitats are evenly distributed or that various size- or age-classes of animals use habitats similarly, both spatially and temporally. Skalski and Robson (1992) discussed the need for using replicate populations in study designs to estimate abundance in geographic areas with spatial heterogeneity.

Despite the problems associated with density estimates for box turtle populations, qualitative comparisons are useful and we calculated two crude density estimates for our study site by simply dividing our abundance estimate at survey 9 for adults and for adults plus juveniles by the area sampled. We arbitrarily selected survey 9 for comparison because there was no effect from transients during this time period. Densities on the southern part of the island were 14.9 turtles/ha for adults only and 16.4 turtles/ha for adults plus juveniles. Because of variation in habitat usage by box turtles on Egmont Key (Dodd et al., 1994), we know that these density estimates are biased. However, our densities fall within the range of estimates at other study sites (Table 6). In most of the habitats studied thus far, eastern box turtles can be locally abundant.

TABLE 6.—Density estimates of box turtle (*Terrapene carolina*) populations based on mark-recapture data from research at other locations.

Subspecies	Locality	Year	Density (No./hectare)	Estimate of variance	Reference
carolina	Indiana	1960–1967	4.4–5.7	No	Williams and Parker, 1987
		1970	3.7		
		1983	2.7		
carolina	Maryland	1950	9.9–12.4	No	Stickel, 1950
bauri	Florida	1993	14.9 (adults only)	Yes	This study
			16.4 (adults + juveniles)		
carolina	Tennessee	1968	18.8–22.7	No	Dolbeer, 1969
triunguis	Missouri	1966–1979	18.4–26.9	Yes	Schwartz et al., 1984

Comparison of our island population to mainland populations of Florida is also problematic. Comparative data are not available and, indeed, a relatively undisturbed mainland population may not exist today because of the intensive urbanization and landscape changes that have occurred and are occurring in peninsular Florida. Carr (1940) described the Florida box turtle as widely distributed and locally common in mainland Florida, although no quantitative estimates were available at the time and perceptions of high abundance on a landscape scale may not be accurate (Dodd and Franz, 1993). Population size on the island could be higher than those of mainland populations if the lack of predators has an effect on population size.

In addition to the estimate of abundance, our analysis also provided information concerning the ecology and behavior of individuals in the population. Survival rates were estimated from the capture data as part of the mark-recapture model. Although these estimates were once thought of as "nuisance parameters" necessary for an unbiased estimate of population size, they are important parameters for understanding life-history strategies and population dynamics (Lebreton et al., 1992). The weekly survival estimates that we calculated appear to be high, but they show a great deal of variability over the relatively short duration of the study (Table 3). This variability could be indicative of changes in mortality regimes that could have significant consequences for the persistence of the island population. Indeed, the lowest weekly survival rate, estimated at period 4, coincided with the survey during which we found carcasses that had been preyed on by a raccoon that had made its way to the island and was subsequently removed (Franz and Dodd, 1993). Rigorous examination of survival patterns for adults and juveniles, however, will require more sophisticated mark-recapture analysis such as that described by Lebreton et al. (1992).

The GOF tests for violations of the assumptions of mark-recapture analysis also showed interesting aspects of the biology of this population. There were no significant differences between adult males and females in capture histories. This was not unexpected, because we found no significant differences between sexes in activity patterns or habitat usage in a previous analysis (Dodd et al., 1994) and weekly survival rates were relatively high (Table 3).

In contrast, there were differences between juveniles and adults in capture histories. Small juveniles are difficult to find in the habitat and may be more susceptible to predation or adverse environmental conditions, such as cold weather, drought, or storm overwash. Most of our direct observations of mortality were of juvenile animals. Stickel (1950) found differences in the number of recaptures of adults and juveniles in her study population in Maryland, suggesting that in addition to the difficulty of finding young individuals, juveniles may travel more extensively than adults.

Perhaps most interesting was the detection of transients during two of the survey periods. One period occurred shortly after the unusually strong spring storm in March 1993. Vegetation on much of the western section of the island was destroyed or modified, causing turtles to relocate; many turtles that we marked near the western beach were later recaptured inland during our survey in April. Why transients were detected in the male segment of the population and not among females is unclear. These movements are in contrast to what Stickel (1950) documented when her study site in Maryland received heavy local flooding and individuals remained in their home ranges. The river flood plain habitat, however, was not inundated with salt water nor drastically altered by the flood. Degradation may not have been severe enough to force turtles to move from the area.

The second period in which transients were detected was in October 1992 when fruiting sea grapes (*Coccoloba uvifera*) attracted turtles to feed at this spatially and temporally restricted food. Our results support the findings by Stickel (1950) and Kiester et al. (1982) that box turtles occasionally temporarily leave their home ranges to travel extended distances. One probable reason for these forays is to feed on a locally abundant food source. Dolbeer (1969) reported that box turtles aggregated to feed on ripe muscadine grapes (*Vitis rotundifolia*) in Tennessee and noted a succession of individuals over a two-day period. Although transients may be important to gene flow in certain continental contiguous populations (Kiester et al., 1982), the effect of transients on population structure in our spatially restricted study site on Egmont Key probably is negligible.

The results of our analysis have illustrated several important features of the new mark-recapture programs that are now available. In addition to estimates of abundance, GOF tests contained in program RELEASE can identify violations of assumptions and provide insight into the accuracy and validity of abundance estimates. Furthermore, these GOF tests along with the probability estimates of capture and survival can identify important aspects of the biology of a population. In many instances, this information may be of equal or greater interest than the actual number describing population size. New advances in mark-recapture analyses continue to be made and computer programs are becoming more user-friendly. Nichols (1992) described some of these advances and the new questions and hypotheses that can now be addressed by biologists who are not necessarily biometricians. Turtle biologists who use mark-recapture techniques could benefit from using these new statistical methods.

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