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Implications of fetal sex ratio hypotheses in endangered populations: simulated dynamics of Florida Key deer, Florida, USA

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Abstract

Fetal sex ratios (FSRs) have important implications for managing small isolated populations. Mean male-biased FSRs ranging from 2.67:1 to 1:1 have been reported for the endangered Florida Key deer (*Odocoileus virginianus clavium*). Several general hypotheses have been proposed that describe the manner in which FSR may vary within a deer population over time: (1) tendency to equalize the sex ratio by producing the minority sex, (2) poor body condition results in more males, and (3) excellent body condition results in more males. Our objective was to evaluate implications of FSR for Key deer as suggested by these hypotheses. Because of their small numbers and geographic isolation, the issue of FSR is important for predicting response of Key deer to management actions. We developed nine alternative deterministic models representing combinations of three mean or median FSRs that have been hypothesized for Key deer and the three hypothesized mechanisms of FSR variation. With each model, we simulated Key deer demographics and compared predictions with actual survey data (1971–2000). The model with the best prediction was based on a median FSR of 1.45:1, and the FSR variation within the survey data best supported the hypothesis that poor body condition would result in more males. Our results indicate the most commonly cited FSR (2.67:1) for Florida Key deer is inaccurate, probably due to small sample size. We conclude that FSR variation has the potential to shape the response of endangered populations to disturbance.

Keywords: Key deer; *Odocoileus virginianus clavium*; Fetal sex ratio; Simulation model; Endangered species

1. Introduction

Fetal sex ratio (FSR) is potentially an important demographic parameter. Models of large metapopulations often ignore FSRs because emigration and immigration can ameliorate potential changes in population sex structure as swings in sex ratio tend to even out over long periods of time, and density-dependent influences on mortality and natality rates can exert a dominating influence on the population dynamics of a species. It also has been argued that population viability analysis models should only contain a level of detail consistent with the data available and should project population dynamics only over short time horizons (Akcakaya and Sjogren-Gulve, 2000). However, in small isolated populations, relatively small changes in FSRs can have a dramatic impact on population dynamics.

Although FSR allocation is poorly understood, some general hypotheses have been proposed. Fisher's

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(1930) sex ratio principle (FP) predicts a genetic tendency to produce offspring of the minority sex. Trivers and Willard (1973) proposed the maternal condition (MC) hypothesis for species with high maternal parental investment (PI) in which mothers in better condition would show a bias towards male offspring. Finally, according to the local resource competition (LRC) hypothesis, mothers should exhibit higher PI in the sex that competes least for limited resources (e.g. food, territory, and mating opportunities) among their offspring and between their offspring and themselves (Clark, 1978; Silk, 1983).

Confounding factors associated with work on large populations combined with the difficulty of interpreting PI with litters >1 (Williams, 1979) have made studying these hypotheses difficult in wild populations. Further, since differential mortality between the sexes is rarely known, the argument that sex-specific mortality might shape population sex structure (Clutton-Brock et al., 1985) rather than FSR allocation is irrefutable. The Florida Key deer provides a unique opportunity to analyze the demographic impact of different FSRs. Current (1998–2000) sex-specific mortality and natality rates are similar to those previously (Silvy, 1975) recorded (1968–1972) when the population was one-third of its current density, according to radiotelemetry and mark-recapture data (Lopez, 2001). Estimates of these population parameters also are available from necropsy data (1966–2000) (United States Fish & Wildlife Service (USFWS), unpublished data). Folk and Klimstra (1991) reported that the Key deer has relatively low potential growth rates due to low natality rates and a hypothesized male-biased FSR. Folk and Klimstra (1991) observed a male-biased FSR with a mean of 2.67:1 in Key deer. Conversely, Lopez (2001) found a less extreme mean male-biased FSR of 1.45:1. Of course, accepting any skewed FSR would require rejecting the null hypothesis of random fluctuation around a mean FSR of 1:1.

Here we describe development of a set of nine simulation models representing the combinations of the three FSR variation hypotheses (FP, MC, LRC) and the three mean (or median) FSRs hypothesized for Key deer (1:1, 1.45:1, and 2.67:1). We then examine the sensitivity of each model to changes in age-specific natality and mortality rates. Next we identify those models capable of simulating the Key deer population trends and FSRs over the 1970–2000 period. Finally, we explore the possibility of generating the historical Key deer population trends with urban development, disease, and/or mortality of deer due to auto collisions rather than variations in FSR.

2. Background

The endangered Florida Key deer, the smallest sub-species of white-tailed deer in the United States, are endemic to the Florida Keys on the southern end of Peninsular Florida (Hardin et al., 1984). The deer's range extends from Big Johnson Key to Sugarloaf Key, although approximately 65–75% reside on Big Pine (the largest of the lower Keys, 2428 ha) and No Name keys (Silvy, 1975; Lopez, 2001). Between 1968 and 1972, there were approximately 250–300 Key deer when the first extensive survey was conducted (Silvy, 1975). During a 1998–2000 survey, the Key deer population had grown to an estimated 700–800 individuals (Lopez, 2001).

Annual population trend data are available from 1976 to the present. The population appears to have peaked around 1978–1979 and again during 1997–2000 (Lopez, 2001). The low numbers around 1981–1986 and 1971–1976 could have several causes, but urban development has been blamed. Habitat fragmentation caused by real-estate development could result in greater movements to meet life history requirements that, in turn, could result in greater highway-associated mortality (Folk and Klimstra, 1991). The increased number of deer-auto collisions, however, might simply result from higher deer densities (Frank, USFWS, personal communication). If this is the case, population oscillations may represent a response to disturbance mediated by FSR.

3. Basic structure of the models

The basic structure of the nine models is identical. Each model consists of four submodels representing (1) female demographics, (2) male demographics, (3) FSR, and (4) habitat changes (Fig. 1). The female and male submodels simulate age-specific mortality and, for females, natality rates. The habitat submodel represents increases or decreases in the number of "hectare equivalents" in each of six habitat types. A "hectare

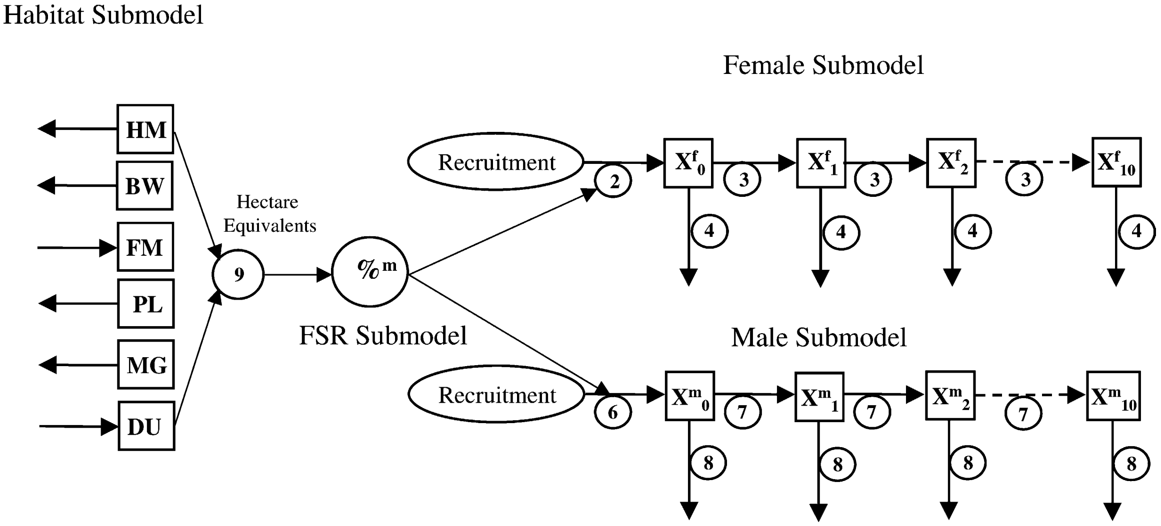

Fig. 1. Basic structure of the simulation models. X_i^{f} and X_i^{m} in the female and male submodels represent the number of females and males, respectively, in the *i*th age class. HM, BW, FM, PL, MG, and DU represent the number of hectares of hammock, buttonwood, freshwater marsh, pineland, mangrove, and developed upland, respectively. $\%^{\mathrm{m}}$ represents proportion male. Numbers inside circles represent equation numbers in the text.

equivalent” is defined as the amount of land that has the same habitat value as 1 ha of hammock habitat (the most preferred habitat of Key deer) (Lopez, 2001). The proportion of land in each habitat type determines total hectare equivalents, which is an index of both quantity and quality of the habitat for Key deer (Lopez, 2001). The FSR submodel determines FSR as a function of population density for MC and LRC variations or uses the mean FSR for FP variations.

4. Quantitative description of the models

The models are represented mathematically as deterministic compartment models based on difference equations with a 1-year time step. Simulations are run on a personal computer using STELLA® II (High Performance Systems, Inc., 1994). All nine models have identical female, male, and habitat submodels; they differ only in their FSR submodels.

4.1. Female submodel

This submodel contains 11 state variables representing the number of female Key deer in age class 0 (fawns), 1 (1 year old), . . . , 10 (10 years old and older), and material transfer equations representing the processes of recruitment, survival (from one age class to the next), and mortality. We present the general form of both state variable and material transfer equations below. In these equations state variables are denoted by uppercase *X*’s, rates of material transfers (recruitment, survivorship, mortality) by lowercase letters, and model parameters (e.g. age-specific natality, mortality) by single lowercase letters. Superscripts refer to sex of the animal and subscripts refer to age class of the animal at a specified time. State variable equations are of the general form:

$$X_{i,i+t}^{\mathrm{f}} = X_{i,t}^{\mathrm{f}} + (\mathrm{input}_{i,t} - \mathrm{output}_{i,t})\Delta t \qquad (1)$$

where $X_{i,t}^{\mathrm{f}}$ is number of females in age class *i* at time *t*, $\mathrm{input}_{i,t}$ is the sum of material transfers into X_i^{f} during the time interval *t* to $t+1$ and represents natality or survivorship from the previous age class, and $\mathrm{output}_{i,t}$ is the sum of material transfers out of X_i^{f} during the time interval *t* to $t+1$ and represents mortality plus survivorship to the next age class. Material transfer equations are as follows:

$$f_t^{\mathrm{f}} = \sum_i \alpha_i X_{i,t}^{\mathrm{f}}(1 - \%^{\mathrm{m}})\mathrm{ri}_t \qquad (2)$$

$$s_{i,t}^{\mathrm{f}} = X_{i,t}^{\mathrm{f}} - m_{i,t}^{\mathrm{f}} \qquad (3)$$

$$m^{\mathrm{f}}_{i,t} = \gamma^{\mathrm{f}}_i X^{\mathrm{f}}_{i,t}\,\mathrm{mi}_t \qquad (4)$$

where f^{f}_t is the number of female fawns born from time t to $t+1$, α_i is the number of fawns born from time t to $t+1$ per female aged i at time t, $\%^{\mathrm{m}}$ is the % of fawns that are male, ri_t represents a density-dependent recruitment index ($\mathrm{ri}_t = 1$, if population density (total number of deer_t/total hectare $\mathrm{equivalents}_t$) < 0.35; $\mathrm{ri}_t = -5 \times \mathrm{density}_t + 2.75$, if population density ≥ 0.35), $s^{\mathrm{f}}_{i,t}$ is number of females aged i surviving from time t to $t+1$, $m^{\mathrm{f}}_{i,t}$ is number of females aged i at time t dying from time t to $t+1$, γ^{f}_i is the proportion of females aged i dying from time t to $t+1$, and mi_t represents a density-dependent mortality index ($\mathrm{mi}_t = 1$, if population density < 0.35; $\mathrm{mi}_t = 5 \times \mathrm{density}_t - 0.753$, if population density ≥ 0.35).

Age-specific survival rates for fawns, yearlings, and adults (Table 1), and natality rates for yearlings and adults (Table 1) are based on corroborating estimates from telemetry studies (1968–1972 and 1998–2000) (Silvy, 1975; Lopez, 2001). The initial, 1970, Key deer population level was 167 animals (Silvy, 1975). Initial sex ratio was set at 1:1 and initial age structure reflected the age-specific survival indicated in Table 1. The mortality ($m^{\mathrm{f}}_{i,t}$) and recruitment (ri_t) indexes have no effect until the population reaches 0.35 deer per hectare equivalent. In 1997, there were between 450 and 550 deer on Big Pine Key (0.22 deer per hectare and 0.35 per hectare equivalent) and natality and survivorship still were equivalent to all other years for which data are available (Lopez, 2001). However, the density of 0.35 deer per hectare equivalent does appear near the point where survivorship and natality are affected as evidenced by signs of malnutrition and disease (Lopez, 2001). We assumed that natality rate decreases linearly and mortality rate increases linearly above this density. Because changes in age-specific survivorship and natality were not detectable between the high and low populations in the range we attempted to simulate (Lopez, 2001), density dependence was only included to prevent exponential growth in models not limited by FSR.

4.2. Male submodel

This submodel contains 11 state variables representing the number of male Key deer in age class 0 (fawns), 1 (1 year old), . . . , 10 (10 years old and older), and material transfer equations representing the processes of recruitment, survival (from one age class to the next), and mortality. The equations are directly analogous to those described in the female submodel:

$$X^{\mathrm{m}}_{i,t+1} = X^{\mathrm{m}}_{i,t} + (\mathrm{input}_{i,t} - \mathrm{output}_{i,t})\Delta t \qquad (5)$$

where $X^{\mathrm{m}}_{i,t}$ is number of males in age class i at time t, $\mathrm{input}_{i,t}$ is the sum of material transfers into X^{m}_i during the time interval t to $t+1$, and $\mathrm{output}_{i,t}$ is the sum of material transfers out of X^{m}_i during the time interval t to $t+1$. Material transfer equations are as follows:

$$f^{\mathrm{m}}_t = \sum_i \alpha_i X^{\mathrm{f}}_{i,t}(\%^{\mathrm{m}})\mathrm{ri}_t \qquad (6)$$

$$s^{\mathrm{m}}_{i,t} = X^{\mathrm{m}}_{i,t} - m^{\mathrm{m}}_{i,t} \qquad (7)$$

$$m^{\mathrm{m}}_{i,t} = \gamma^{\mathrm{m}}_i X^{\mathrm{m}}_{i,t}\,\mathrm{mi}_t \qquad (8)$$

where f^{m}_t is the number of male fawns born from time t to $t+1$, α_i is the number of fawns born from time t to $t+1$ per female aged i at time t, $\%^{\mathrm{m}}$ is the proportion of fawns that are male, $s^{\mathrm{m}}_{i,t}$ is number of males aged i surviving from time t to $t+1$, $m^{\mathrm{m}}_{i,t}$ is number of males aged i at time t dying from time t to $t+1$, and γ^{m}_i is the proportion of males aged i dying from time t to $t+1$. Age-specific survival rates for fawns, yearlings, and

Table 1
Age- and sex-specific survival and natality rates for Key deer ± S.D. used in the simulation models (1998–2000) (Lopez, 2001)

Stage	Female		Male
	Survival	Natality	Survival
Fawn	0.6151 ± 0.1495	0	0.7433 ± 0.1103
Yearling	0.8241 ± 0.0713	1.0500 ± 0.0861	0.5689 ± 0.0890
Adult	0.8420 ± 0.0302	1.0500 ± 0.0861	0.5973 ± 0.0544

Mean values are used in the baseline versions of the models; standard deviations provide the ranges over which model parameters were varied during sensitivity analysis.

adults (Table 1) are based on corroborating estimates from telemetry studies (1968–1972 and 1998–2000) (Silvy, 1975; Lopez, 2001).

4.3. Fetal sex ratio submodel

This submodel is parameterized differently for each of the nine models with regard to (1) the mean FSR for the FP variation hypothesis, or the median FSR for the MC and LRC hypotheses and (2) the density-dependent response of each FSR (Fig. 2). The mean FSR of those MC and LRC models predicting constantly high or low densities will not reflect the FSR being tested. By testing medians for these models we avoid the false assumption that mean FSR of model output resembles the FSR being tested. Thus, median FSR, central to a hypothesized range, was tested for MC and LRC models.

The density-dependent response of the MC and LRC FSRs are calculated with linear equations bounded by ±50% of the median in the study population FSR (Fig. 2). There are no data with which to confirm or reject the hypothesis that the relationship between FSR and population density is linear, however, modification of the lines in Fig. 2 such that they are convex or concave does not noticeably change the simulated population trends.

The potential range of variation in FSR is based on data from a pen study of white-tailed deer (Verme and Ozoga, 1981). The $\%^{m}$ attains its minimum at a

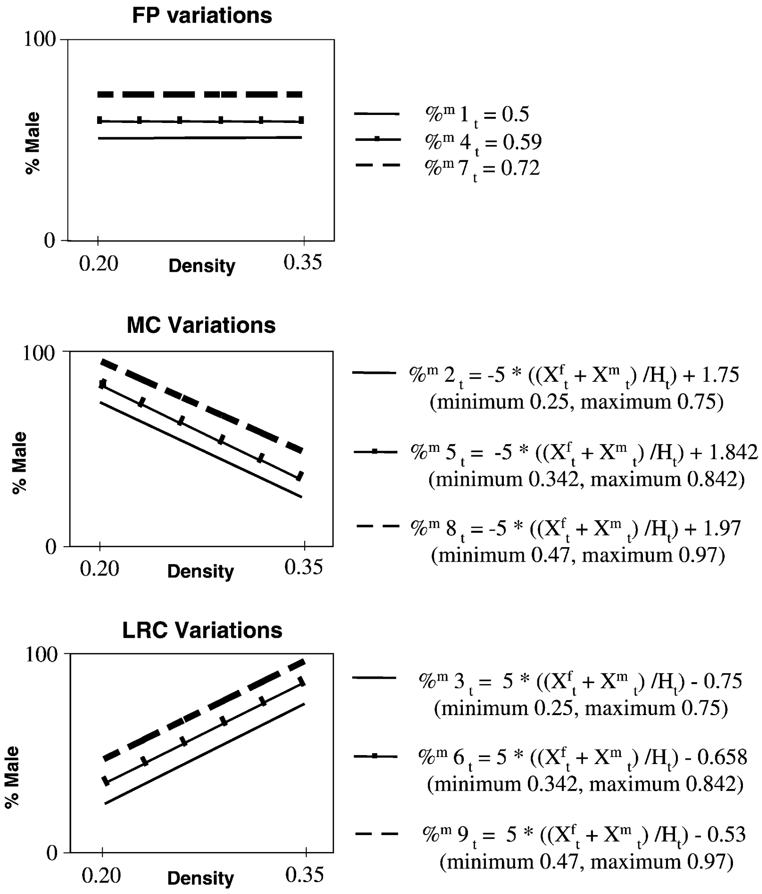

Fig. 2. Graphs representing the relationship between density and proportion male $\%^{m}$ for the nine models simulating FSRs. Relationships 1–3, 4–6, and 7–9 represent 1:1, 1.45:1, and 2.67:1 male-biased FSRs, respectively. FP, MC, and LRC refer to Fisher's principle, MC hypothesis, and LRC hypothesis, respectively. Where H_t is the number of hectare equivalents at time t and X_t^{f} and X_t^{m} are the total numbers of female and male Key deer, respectively, at time t.

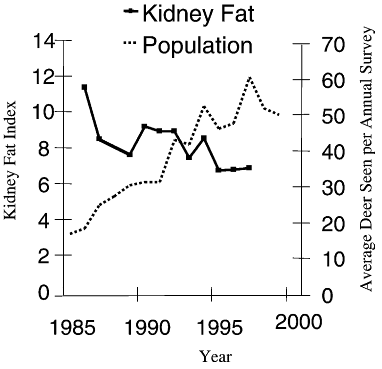

Fig. 3. Graph comparing Key deer population trend data to kidney fat indexes 1986–1997 (USFWS, unpublished data).

density of 0.35 for MC models and a density of 0.2 for LRC models, and attains its maximum at a density of 0.2 for MC models and a density of 0.35 for LRC models. This range of densities represents the highest and lowest known densities of Key deer observed (Lopez, 2001). The density dependency of FSR is based on the assumption that MC is inversely related to population density over the range of densities simulated by our models. Kidney fat indexes from Key deer necropsy data (USFWS, unpublished data) support this assumption (Fig. 3).

4.4. Habitat submodel

This submodel contains six driving variables representing the number of hectares in each of the six habitat types present on the study area. The relative value to Key deer of each habitat type was based on habitat use and availability data gathered from a telemetry study and is highest for hammock and lowest for mangrove (Lopez, 2001). We assigned a “hectare equivalent” adjustment factor to each habitat type based on its value relative to hammock. Hectare equivalent values for hammock (HM), buttonwood (BW), freshwater marsh (FM), pineland (PL), mangrove (MG), and developed upland (DU) are: 1, 0.341, 0.492, 0.884, 0.195, 0.492, respectively (Lopez, 2001). Consequently, the number of hectare equivalents at time t (H_t) is calculated as:

$$H_t = \mathrm{BW}_t \times 0.341 + \mathrm{FM}_t \times 0.492 + \mathrm{PL}_t \times 0.884 + \mathrm{HM}_t \times 1 + \mathrm{MG}_t \times 0.195 + \mathrm{DU}_t \times 0.492 \tag{9}$$

where BW_t, FM_t, PL_t, HM_t, MG_t, DU_t, represent the number of hectares in the indicated habitat type at time t. The initial hectares in each habitat type were: HM = 305.9, BW = 300.3, FM = 236.7, PL = 753.3, MG = 632.8 and DU = 329.1. The number of hectares lost per year (gained by DU and FM) is calculated as its total change in number of hectares over the last 30 years (HM = 81.88, BW = 34.33, FM = 2.29, PL = 166.62, MG = 37.15, DU = 281.45) times the proportion of the total number of hectares lost to urban development during the last 30 years that was lost during the given year (Table 2), where DU and FM are gaining and the other habitats are loosing hectares. The total hectares gained by FM and DU (283.7) does not equal the total hectares lost by other habitat types (320.0) because, footprints of buildings

Table 2
Proportion of the total number of hectares lost to urban development over the last 30 years that was lost in the indicated year (Monroe County Property Appraiser, 2002 Tax Roll Database)

Year	%
1971	0.0211
1972	0.0336
1973	0.0336
1974	0.0316
1975	0.0307
1976	0.0336
1977	0.0230
1978	0.0403
1979	0.0561
1980	0.0374
1981	0.0417
1982	0.0244
1983	0.0402
1984	0.0508
1985	0.0714
1986	0.0642
1987	0.0657
1988	0.0633
1989	0.0599
1990	0.0412
1991	0.0259
1992	0.0244
1993	0.0230
1994	0.0211
1995	0.0216
1996	0.0081
1997	0.0063
1998	0.0053
1999	0.0005
2000	0

were excluded from DU (Lopez, 2001). Freshwater marsh grew in area at the same rate as DU because, gain in FM was a function of gravel pit (used to provide fill for urban development) expansion.

5. Evaluation of models

5.1. Sensitivity analysis

Each of the nine models was robust to changes in age-specific natality and mortality rates. Altering them within the range of standard deviations indicated (Table 1) had little effect on Key deer population trends. Changing the density at which mortality rates begin to increase and natality rates begin to decrease, however, did influence results.

As previously mentioned, when density-dependent factors begin shaping the population they take the dominant role away from FSR. Thus, model 3 exhibited a growth curve similar to models 1 and 4 because it had the highest growth rate of the LRC models and density-dependent changes in natality and mortality rates obscured the trend a LRC model typically predicts (Fig. 4). Lowering the threshold density required to increase mortality and decrease natality rates produces a trend similar to that seen in model 4 for models 6 and 9, respectively, as that threshold drops. Accordingly, raising the threshold would eventually produce a dampened oscillation in model 4.

5.2. Comparing alternative models

To evaluate the performance of our nine models, we compared simulated population dynamics to observed population growth trends (USFWS, unpublished data) and the population change estimated between 1975 and 2000 (Lopez, 2001). Due to the non-linear nature of population growth trends in the Key deer population (1976–2000) (Lopez, 2001), results of model simulations were visually compared to observed growth trends. Models 2, 5, 7, and 8 were poor fits of the observed Key deer population growth trend data model 6 appeared to give the best fit, but models 1, 3, 4 and 9 were plausible (Fig. 4). The 240% increase in the Key deer population between 1975 and 2000 supports elimination of models 2, 5, 7, and 8, since these models predict population decline (Fig. 4).

Comparison to actual FSRs is difficult due to gaps in data. However, necropsy data were taken for 13 years of the last 30 and the average male to female ratio of 1.45:1 (Lopez, 2001) supports models 6 and 4 while contradicting models 1, 3, and 9. Ten of the 13 years of data were not included in the previous estimate of FSR (Folk and Klimstra, 1991), so the recent estimate is probably more appropriate for evaluating models. Yearly trends in FSR were inconclusive due in part to small sample size ($N = 6$–11 per year) and large gaps in the data.

The preference of model 6 over model 4 is supported by mortality data. Because mortality and recruitment rates have not changed dramatically over time (Silvy, 1975; Lopez, 2001), annual mortality should resemble total population size, at field data indicate (Fig. 5a). The oscillation indicated by mortality data supports the LRC hypothesis in another less obvious way. Key deer males have higher mortality than females (Table 1) (Silvy, 1975; Lopez, 2001); so, a male bias in the population will lead to higher mortality than expected if the population had a 1:1 sex ratio and vice versa. Our LRC model 6 correctly predicts lower mortality relative to population size after periods of low-density and female-biased FSR (Fig. 5b, A), and higher mortality relative to population size after periods of high density and male-biased FSR (Fig 5b, B).

Some propose the MC only applies at the individual level, and that population responses can be explained with higher newborn male mortality (Fisher, 1930; Kojola, 1997). Changing the male fawn mortality rate from 0.26 to 0.60, however, only made MC FSRs less plausible because it continues to reduce the already low-density population. This change had negligible effect on LRC FSRs. Further, the MC hypothesis depends on females biasing sex ratios of young based on their deviation from a female mean condition. This condition depends on forage, and with the exception of old, diseased, or otherwise weakened individuals, females will respond similarly to the fluctuations in forage resources.

6. Possible alternative causes

To avoid assuming a causal relationship between our best model and the observed trends in Key deer abundance we considered factors not involving FSR:

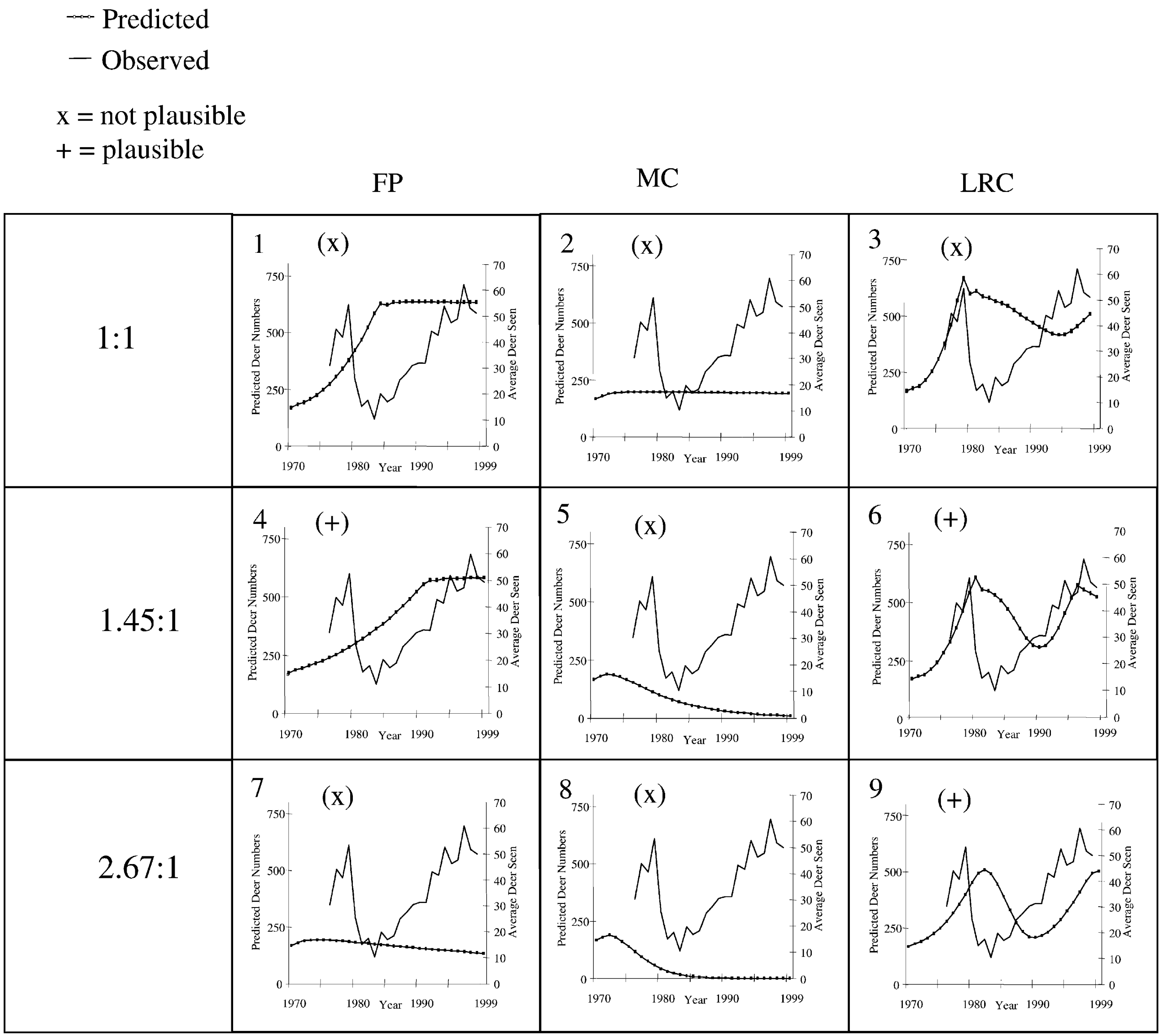

Fig. 4. Comparison of population trends predicted by each of nine models (predicted deer numbers) to population trends observed by USFWS (average deer seen on annual census) from 1976–2000 (USFWS, unpublished data). Numbers in the left margin of the figure refer to the mean FSR. FP, MC, and LRC refer to Fisher's principle, MC, and LRC versions of FSR response to density, respectively. Scale of *y*-axes in graphs were selected so maximum average deer seen approximated estimated carrying capacity.

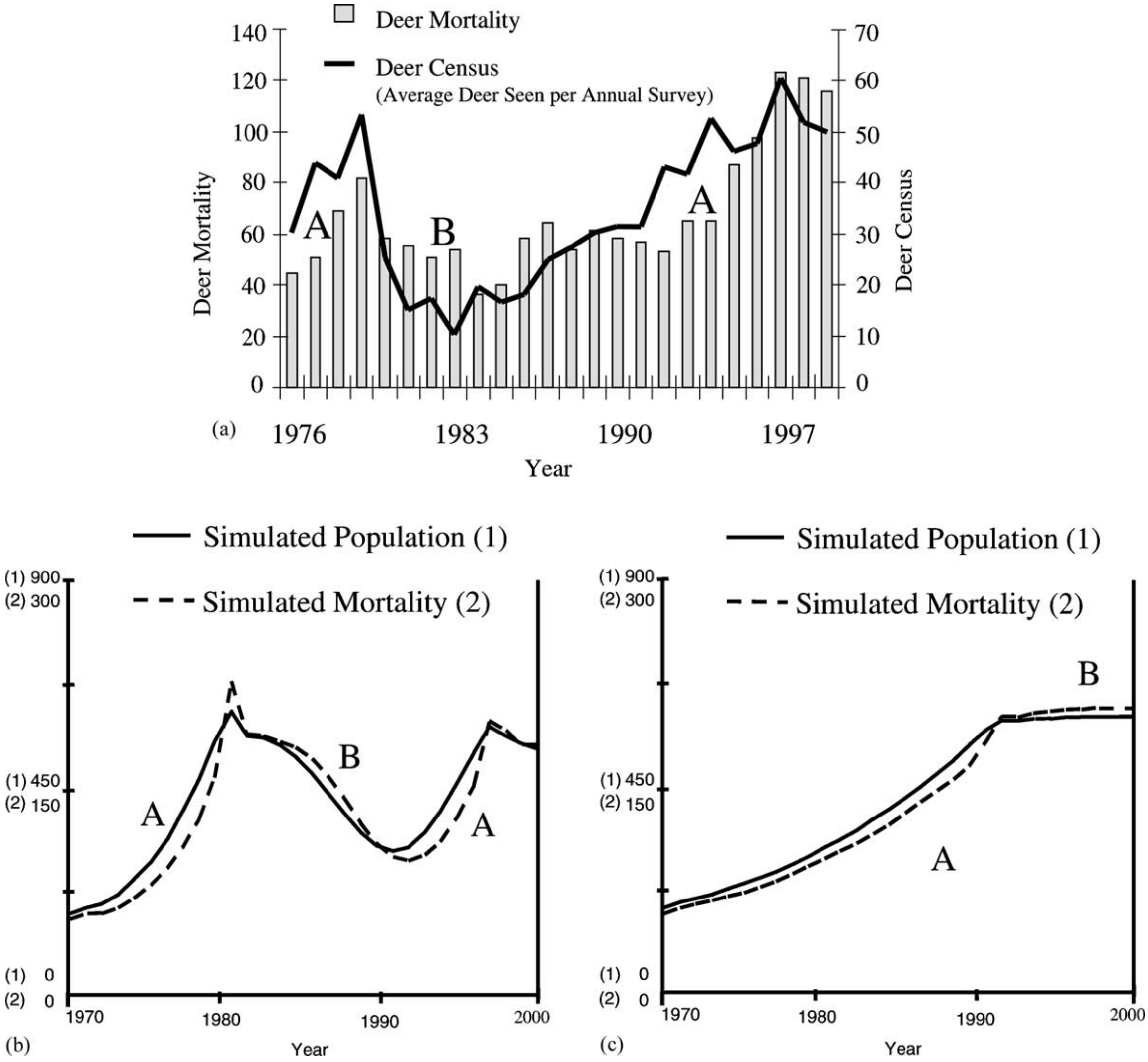

Fig. 5. Comparison of annual Key deer mortality numbers (1976–1999) and population trends: (a) observed trend and mortality, (b) trend and mortality predicted by model 6, and (c) trend and mortality predicted by model 4. A and B refer to areas of low mortality related to female bias in the population and high mortality related to male bias in the population, respectively. Scales of *y*-axes were adjusted to facilitate comparison of trends in the two curves.

development, disease, auto collisions, and density-dependent changes in natality and mortality rates. We determined that human development itself was not a determining factor because when we doubled the recorded development rate, it did not produce a negative growth rate for the deer herd in models (1 and 4) that had stable deer population growth rates under standard conditions. Since disease only accounted for 10% of Key deer mortality throughout the simulation period (Lopez, 2001), it is unlikely that this parameter controlled the oscillations. Because auto-kill levels followed decreases in population rather than preceding them (Fig. 5a), auto-kill appears dependent on population size rather than vice versa. Finally, density-dependent changes in natality and mortality were also unlikely to direct population swings because, as previously noted, these parameters were similar in a period of population growth (1970–1975) and a period of stability or potential decline (1997–2000) (Lopez, 2001).

7. Discussion

The model based on the previously accepted male-biased FSR with a mean of 2.67:1 (Folk and Klimstra, 1991; Hardin et al., 1984) does not reflect the population increase observed in the last 30 years (Fig. 4, model 7). Folk and Klimstra (1991) suggested the LRC hypothesis was influential in producing the skewed FSR, however, the reported FSR of 2.67:1 was a mean of previous years. The LRC version of a median FSR of 2.67:1 only produced a population increase because its mean FSR was 1.8:1 (Fig. 4, model 9). Thus, the previously accepted view of FSR in Key deer cannot be reconciled with observed population growth rates.

Model 6 (a LRC model) best represented the FSR allocation in Key deer. This result has several important implications. First, it supports the view that FSR works according to the LRC hypothesis in Key deer. This in turn supports the hypothesis that deer can control herd size in the face of fluctuating and patchy food sources (Peterle, 1975) because at low densities more females are produced, leading to higher population growth rates and at high densities more males are produced which leads to a decrease in population growth rate. Planned translocation of Key deer to uninhabited islands in the immediate future may provide an opportunity for field research to test the FSR hypothesis represented by model 6. Further, the isolated nature of the Key deer population could have given more weight to evolutionary pressures favoring LRC FSR allocation. This should not be misconstrued as "self-regulation" because density indirectly controls FSR through female body condition. The decrease in recruitment resulting from male-biased FSR at high densities may influence population response to density to a greater degree than decreased natality or increased mortality. Small population size and low potential growth rates give FSR allocation more influence over Key deer population dynamics relative to other density-dependent factors. In fact, Lopez (2001) demonstrated that the population stabilized after a 240% increase without significantly altering mortality and natality rates from 1970s levels (Silvy, 1975).

The influential role of FSR in Key deer population dynamics has important management implications. The main management objective for Key deer is preventing extinction. Catastrophic events such as a category 4 hurricane or disease epidemic are the only serious threats to population viability (Lopez, 2001). Both the small population left after such a cataclysm and small populations created through relocation efforts should respond with dampened oscillations as predicted by model 6. These dynamics exist because when the population is above its equilibrium density, where the LRC hypothesis predicts a male-biased FSR, males are loaded into the population resulting in progressively lower per capita reproductive rates for the population. Because Key deer are relatively long-lived there is a time lag before the sex ratio of the entire population equalizes to a point where positive growth rates occur again.

Model 6 has important implications for USFWS public relations. It suggests the population will stabilize at levels higher than those observed in the 1980s, but that an epidemic disease or other disturbance could set off another series of dampened oscillations. The proponents of preservation and refuge expansion, who argue the population is currently on the top of a recurring oscillation and that management should be based on the next projected low (Peterson et al., 2002), would be correct in some cases. The concern for managing for projected lows would be important after large disturbances. However, oscillations should become progressively smaller and less important. Proponents of private property rights, who argue that the population is stable at its current high levels (Peterson et al., 2002), also would be correct. Future oscillations should be relatively small and insignificant. Basing management strategies on this view would be safe until a large disturbance lowers the population below its equilibrium level. Armed with an understanding of model 6 and its implications USFWS could take a "you are both right" approach.

Understanding the mechanisms of FSR control provides other management opportunities. For Key deer, timing of fertilization within estrous may control FSR. Werren and Charnov (1978) found that a delay in mating during the estrous period caused an increase in the proportion of male progeny in many organisms. Verme and Ozoga (1981) found in white-tailed deer, early matings (13–24 h) in the estrous period resulted in 14.3% males in the fawn crop ($N = 28$) whereas matings consummated late (49–95 h) in the estrous period produced 80.8% males in the fawn crop ($N = 26$). Guerrero (1975) suggested that changes in vaginal and intra-cervical pH that occur around the time of ovulation differentially affect the motility of X- and Y-bearing spermatozoa and are able to influence the FSR. Harlap (1979) suggested the FSR variations were influenced by differential resistance of either sex to problems during embryonic development (e.g. chromosomal abnormalities, blastocystic death, blighted ova) linked to fertilization of older ova or by older sperm.

Little consensus exists regarding FSR allocation in animals, and its influence is usually ignored in managing and simulating wildlife populations. In most cases this approach is not problematic because other population parameters confound the influence of FSR and or approximate it. However, in some cases like that of the Key deer, FSR may exert a dominant influence over population dynamics. Other endangered (isolated) animal populations that exhibit LRC FSRs may react to disturbance like the Key deer. K-selected species in particular will respond in a similar manner. Oscillations in a more r-selected population will have high frequencies that make monitoring and response more difficult.

Small population size, isolation, and low reproductive rates will magnify the influence FSR maintains in the population. Accordingly, many endangered animal populations cannot be accurately simulated without consideration of FSR allocation. Population viability analyses should consider all feasible scenarios (Beissinger and Westphal, 1998), and FSR variation having a controlling influence on population dynamics is feasible. Regardless of the FSR mechanism in operation for a particular species (FP, MC, or LRC) influencing the breeding population to produce an excess of the sex limiting reproduction can accelerate captive breeding. Further, the management implications and strategy suggested by simulations under assumptions of different FSR allocation mechanisms will be extremely different (Fig. 4). FSR and the mechanism of allocation should be considered when managing endangered animal populations.

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