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A dynamic game model for the decision to join an aggregation

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Abstract

A dynamic game model is presented for the decision-making of female saiga antelopes (*Saiga tatarica*) gathering in temporary aggregations to give birth. Spatial aggregation is assumed to be a predator-swamping mechanism that involves a cost of an increased risk of calf death from disease. A female's decision to join an aggregation or to calve solitarily depends on her parturition date relative to other individuals and on the number of other females in the birth area. The results are robust to changes in other parameter values. The Evolutionarily Stable Strategy is to join an aggregation and stay for the full period of neonatal vulnerability if calving early in the birth period, to join the aggregation but to leave it early if calving later in the birth period, and to calve solitarily if calving at the end of the birth period. The possible effects of human disturbance on female behaviour are investigated, and testable hypotheses are presented about the behaviour of females in the birth period. The game-theoretic approach to the decision to join an aggregation developed here is broadly applicable to many problems in the ecology of grouping behaviour. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Saiga antelope; Group living; Predation; Disease; Trade-offs

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1. Introduction

Optimisation models of decision-making by animals and humans have been widely used to examine the factors influencing decisions in an uncertain environment (Krebs and Davies, 1984; Mangel and Clark, 1988; Mace and Houston, 1989; Houston and McNamara, 1999). Game theory has been used in the case when an individual's decision is not independent of the decisions of those around them (Maynard-Smith, 1982; Mesterton-Gibbons and Adams, 1998; Pontier et al., 2000). Individuals who join aggregations are making decisions in the context of decision-making by others; hence, game theory is an appropriate tool for modelling group formation in ecology.

The issue of optimal behaviour by animals joining groups has not been much modelled, despite the large body of experimental work on the subject (Mooring and Hart, 1992; Krause, 1994) and

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the influential early work of Hamilton (1971) and has rarely been addressed using a game-theoretic framework. Rubenstein (1978) developed a theoretical framework for exploring evolutionarily stable strategies of group living for dominant and sub-dominant individuals, while Turner and Pitcher (1986) developed a model of the benefits of joining a group under predation pressure. In a similar vein, Mangel and Clark (1988) used stochastic dynamic programming to predict group size in foraging lions. There has also been some modelling of grouping behaviour when individual behaviour depends not on the behaviour of others but on quantities such as distance to the nearest neighbour or group size (e.g. Seno and Nakai, 1995; Yamazaki and Okubo, 1995).

In this paper, I present a model of the decision to join an aggregation, in the form of a deterministic dynamic game. This framework has the advantage of allowing the decison to join a group to be taken on the basis of the expected behaviour of other individuals, within the context of a trade-off between key factors determining the costs and benefits of joining a group.

Many species show spatial and temporal aggregation during breeding (Patterson, 1965; Boness et al., 1995). This is often attributed to seasonal availability of food resources and/or predator avoidance; Rutberg (1987) showed that both the degree of seasonality of a habitat and juvenile vulnerability to predators were correlated with the degree of birth synchrony in 27 ungulate species. Joining an aggregation has both costs and benefits (Brown and Brown, 1986, 1987), and the individual's decision as to whether it is best to join the aggregation or to remain solitary is thus a trade-off, the results of which may vary with an individual's dominance rank or with environmental conditions (Rubenstein, 1978).

The saiga antelope (*Saiga tatarica*), a nomadic, herding species of the semi-deserts and steppes of Central Asia, forms large temporary aggregations to give birth. Although the vast majority of females give birth in aggregations, females are sometimes observed giving birth solitarily, particularly young females calving late in the birth period. This observation gives rise to the question of what determines an individual female's decision to join an aggregation to calve, and what factors might act to influence that decision. The model presented here is of a female saiga's decision to join an aggregation or calve solitarily, made at the point of parturition and dependent on the trade-off between the risks of calf mortality from predation and disease. The behaviour that an actively optimising female might adopt in response to human disturbance is discussed, and the results are related to observations of saiga behaviour.

2. Trade-offs in joining an aggregation

Saiga antelopes show both temporal and spatial clustering of births. They gather in spring in areas where there is good pasture, accessible water and minimal disturbance (Bekenov et al., 1998). They are distributed relatively evenly across these calving areas, at an average density of five to seven calves per hectare (Fadeev and Sludskiy, 1982). Birth takes place between late April and early June, with mass calving occuring over a short period (3–8 days, Fadeev and Sludskiy, 1982). Calves remain hidden for the first 2 days. At the age of 4–5 days, the calves move with their mothers to the periphery of the birth area, and at 8–10 days, they move off to the summer pastures (Bannikov, 1961; Sludskiy, 1962). Observations suggest that the maximum potential size and location of a saiga aggregation are determined by the quality of the forage and water supplies available in an area, and that these vary from year to year according to the climate (Iu.A. Grachev, pers. commun.; Sludskiy, 1962). The typical size of a large aggregation is 50 000–150 000 animals (25–75% of the population); there may be two or three of these large aggregations with the rest of the population in smaller groups.

Temporal clustering of births can be a mechanism for the optimal exploitation of seasonal food resources (Rutberg, 1987). This is particularly likely to be the case for saiga antelopes, living in a highly seasonal steppe/semi-desert ecosystem. The peak biomass of steppe vegetation occurs in May or June, and forage quality declines rapidly in the dry summer, suggesting that early calving would be advantageous. However, the earliest calving date is limited by the weather in early spring; a significant proportion of calves die in the first days of life from cold rain, hail and overnight frosts. Data on the temporal aggregation of saigas are available from expeditions undertaken to tag newborns by the Institute of Zoology of the Kazakhstan Academy of Sciences between 1986 and 1993. The number of juvenile saigas captured each day rises to a peak and then declines over a period of about 6 days (Fig. 1).

2.1. Predators

The spatial clustering of saigas is likely to be a predator-swamping mechanism. Saiga calves are vulnerable to various predators in the first few days of life, particularly wolves. These can be major causes of calf mortality; a wolf was observed killing five calves in the space of 1 h, and transects carried out in calving areas between 1965 and 1976 revealed that 0.5–3 calves/km had been killed by wolves (Fadeev and Sludskiy, 1982). By the age of 4–5 days, calves can run away from predators, and by the age of 8 days, they are capable of out-running a wolf (Fadeev and Sludskiy, 1982).

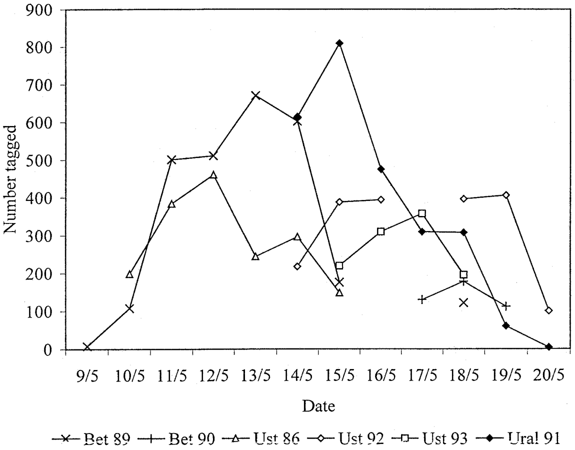

Fig. 1. Data on the number of newborn saigas tagged each day on expeditions carried out by the Institute of Zoology and Animal Genetics of the Kazakhstan Academy of Sciences, in May 1986–1993 (Iu.A. Grachev, pers. commun.). Three saiga populations were visited: Betpak-dala ('Bet'), Ustiurt ('Ust') and Ural. The legend shows the population and the year for each data set. The difficulty of capturing juveniles increases with age; those older than 2 days are rarely caught. Thus, although the figure does not show the true distribution of birth dates, the confounding effect of individuals of different ages being caught is limited. Variation in sampling effort from year to year and from day to day within a year is not quantifiable but is minimised by the same team carrying out the work each year and working for about the same length of time each day. Differences in peak birth dates between the datasets reflects both inter-annual variability in climatic conditions within a population and the fact that the further east a population is, the later it tends to calve (Bekenov et al., 1998).

Wolves have been observed following migrating herds, particularly in winter. However at the time of saiga births, they maintain territories in which they raise their young (Sludskiy, 1962; Fedosenko et al., 1985). Thus, there is no numerical response by wolves in saiga birth areas; wolves have been observed not to predate saiga herds gathered only a few kilometres outside their territory (Fedosenko et al., 1985). Wolves need to remain close to water in the spring; thus, the location of saiga birth aggregations far from water sources has been interpreted as evidence for the importance of wolves as predators of juvenile saigas (Sokolov and Zhirnov, 1998), because females incur the daily cost of travelling to the water source.

2.2. Disease

Parasites have been cited both as factors promoting group living (Mooring and Hart, 1992) and as costs of group living (Brown and Brown, 1986). Because of the highly seasonal climate and the migratory nature of the saiga, parasite transmission is likely to be concentrated during the birth period, and thus to be a cost of aggregation, as are infectious diseases. Foot-and-mouth Disease (FMD) can cause high mortality in saiga calves, unlike in adults. There were six outbreaks of FMD between 1955 and 1974. The most serious was in 1967, when the disease spread over an area of more than 100 000 km^2, resulting in the deaths of about 50 000 calves, with 2–26 corpses/km^2 (Bekenov et al., 1998). Mass vaccination of livestock for FMD started in 1974, and there has not been a recorded outbreak in saigas since then. However, since the independence of Kazakhstan in 1991, FMD vaccination has been carried out less reliably, and there have been outbreaks reported in livestock (Lundervold 2001). Data from 1996–1998 show sero-positives to FMD in livestock, mostly due to vaccination but some due to infection, although no sero-positives to FMD were found among saigas (Lundervold 2001). This suggests that FMD is epidemic rather than endemic among saigas and is probably transmitted to saigas from livestock, and that saigas are currently susceptible to FMD.

FMD is extremely contagious; if it infects one member of an aggregation, all current and future members of that aggregation have a high risk of exposure to the disease (Donaldson, 1987). The more females join the aggregation, the higher the risk that one of them has been infected. Most parasites and diseases that carry a risk of calf mortality have a similar pattern to FMD; the more females that have congregated in an area, the higher the risk to a recently born calf. Thus, although FMD is used as an example, the model predictions are general.

2.3. Effects of human disturbance

Hunting during the rut causes disturbance during mating, and selection for adult males leads to a lack of experienced males. Both of these may lengthen the mating period, and therefore the birth period, causing increased juvenile mortality either through less effective predator-swamping or sub-optimal timing relative to forage availability (Ginsberg and Milner-Gulland, 1994). During the birth period itself, human disturbance from hunting or dogs can cause aggregations to break up and increase calf mortality. Surveys in 1989–1993 suggested that about 6.8% of saiga calves died at birth or in the first few days of life; 50% of these deaths were attributable to human disturbance (Bekenov et al., 1998).

The recent collapse in livestock numbers in saiga range areas has led to increased saiga hunting, which is a major cause of disturbance (Robinson, 2000). However, the reduction in livestock numbers may mitigate the increased chance of an FMD outbreak caused by unvaccinated livestock. Previously, saiga managers culled wolves to protect saiga herds; since independence, a lack of funds has curtailed this, and wolf densities are now high (V.V. Ukrainskiy, pers. commun.). Observations from 1996 to 1998 suggest that there are major differences between two of Kazakhstan's saiga populations. The Ustiurt saiga population is relatively undisturbed, and still has large, dense birth aggregations. The Betpak-dala population is heavily poached and has looser birth aggregations made up of many fewer females (Lundervold, 2001).

2.4. Female decision-making

A female saiga's parturition date, which determines her position in the temporal clustering of births, is determined by her mating date during the rut. Saigas have a harem breeding system, where dominant males defend harems of up to 30 females. Females become sexually mature at 8 months and routinely twin, except in their first year when they generally give birth to single calves (Bekenov et al., 1998). A female's parturition date relative to others is likely to be determined by her dominance within the harem, which may be linked to her age. No studies of saiga behaviour during the rut have been carried out, so the details of dominance relationships are still unclear.

Although she may not be able to influence the date on which her calf is born, a female can influence her calf's spatial location by deciding whether to give birth within an aggregation or solitarily. Spatial position influences the probability of calf death from predation (through predator-swamping) and disease (particularly FMD, through contact with other infected individuals). Both of these interact with parturition date, so that a female's decision to join an aggregation may be influenced by her parturition date relative to the other females in the aggregation. Once the female has made her decision, it is irreversible for the first three days of life, because the calf is immobile.

Table 1
Parameters used in the female choice model

Parameter	Symbol	Baseline value [a]	Range [a]
Maximum number of females that could potentially arrive in the birth area	N_{max}	75 000	75 000–100 000
Total number of females actually arriving in the birth area	N_{tot}	50 000	5000–100 000
Number of calves per female	–	1	–
Number of days on which females give birth	–	14	–
Number of days a calf is immobile	–	3	–
Maximum number of days a calf stays in a aggregation	–	6	–
Maximum number of calves killed by wolves in a day	W	400	100–800
Rate of increase of number killed with herd size	q	0.5	0.33–1
Rate of change in susceptibility to predation with calf age	α	0.3	–
Daily probability of being killed by disease, solitary calf	d_0	0.0125	0.025–0.0083
Rate of increase in disease risk with aggregation size	β	2	–
Constant in gamma distribution	c	4	3[b]
Constant in gamma distribution	a	1	2[b]

[a] The baseline values are those used in the original model, and the range is that over which the parameters are varied in the sensitivity analyses.

[b] Two gamma distributions were tested: the baseline case ($c = 4$, $a = 1$), and a case where $c = 3$, $a = 2$.

3. Model of female choice

3.1. Number of births

Each day, a given number of females is assumed to arrive in the birth area, and each gives birth to one calf. Hence, the number of females arriving is equivalent to the number of births on a given day. Although saigas generally twin, twins lie together and are thus at a similar risk of mortality from predation and disease; this allows the simplification of considering them as a single individual. Although this assumption does not capture the difference in the number of calves produced by first-year and older females, it allows decision-making to be expressed in a more general framework. Quantitative data are not available to relate the number of individuals arriving in an area to any particular factors, so the number of females arriving in an area is varied in sensitivity analyses (Table 1). Because birth date has a skewed distribution, with a marked peak and a tail, it is modelled using a gamma distribution (Eq. (1)). This distribution has a long tail, is flexible enough in shape to allow a number of possible birth date distributions to be investigated, and takes only non-negative values (Hilborn and Mangel, 1997). The number of births on a given day, t, is given by:

$$b_t = N_{tot}\frac{a^c}{\Gamma(c)}e^{-at}t^{c-1} \qquad (1)$$

where: b_t = number of births on day t ($1 \le t \le 14$); N_{tot} = total number of females arriving in the birth area over the whole period; a, c are constants.

The distribution of birth dates under the baseline parameter values (Table 1) is shown in Fig. 2. The Gamma distribution is not fitted to the data

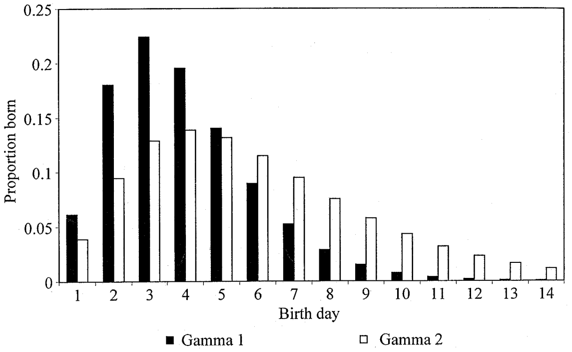

Fig. 2. Distribution of birth dates obtained from the gamma distribution (Table 1, Eq. (1)). The base case distribution ('Gamma 1') is peaked on the 3rd day, with a long tail; this has constants $c = 4$, $a = 1$. A distribution with a later peak and more spread ('Gamma 2', $c = 3$, $a = 2$) is also tested; this represents a possible scenario for the current situation in Betpak-dala.

presented in Fig. 1 because of the problems with the interpretation of the data outlined above. The effect of heavy hunting or other disturbance is tested for by reducing the total number arriving at the site and by changing the parameters of the gamma distribution.

3.2. Predation

Females are assumed to aggregate to give birth as a predator-swamping mechanism. The total number of calves killed by predators each day is assumed to vary with the number of calves in the aggregation according to Eq. (2), which describes a Type II functional response to prey density:

$$k_t = \frac{WN_t}{q^{-1}W + N_t} \tag{2}$$

where: k_t = number of calves killed by predators on day t; W = maximum number of calves that the predators can kill in a day; N_t = size of the aggregation (total number of calves of all ages present on day t); q = maximum rate of increase of number killed with herd size.

This type of functional response was shown by Ims (1990) to favour reproductive synchrony as a predator-swamping mechanism. To represent the increasing ability of saiga calves to escape from predators with age, an exponential decline in susceptibility with age is assumed. The distribution of animals killed between age classes is calculated as:

$$s_A = ze^{-\alpha A} \tag{3}$$

where: s_A = susceptibility to predation; A = age of the calf in days ($1 \leq A \leq 6$); α = rate of change of susceptibility with age; z = normalisation coefficient (such that $\Sigma_A s_A = 1$).

The daily predation risk for a solitary calf is calculated as $w_{t,A} = k_t s_A$ where $N_t = 1$. For calves in an aggregation, the total number killed is calculated according to Eq. (2). These deaths are distributed among age classes, weighted according to Eq. (3). In classes where the number killed exceeds the number available, the surplus deaths are iteratively redistributed among the remaining classes according to susceptibility. The predation risk for each age class, $w_{t,A}$, is then calculated as the number killed divided by the number in the class.

Predation is assumed to be frequency-dependent, but predators do not specifically target large herds over solitary individuals. Although large aggregations are likely to be more noticeable to predators than solitary individuals, this assumption suffices because the solitary individuals tend to be found in the vicinity of aggregations. If predators find an aggregation, they take the maximum number of individuals possible, given the constraints of Eq. (2). The paucity of data makes it impossible to estimate calf mortality from predation, so parameter values were chosen to concord with authors' qualitative statements that predators are a significant cause of calf mortality in small groups, but have a negligible effect in large aggregations (Table 1). Fedosenko et al., (1985) say that in the spring, wolves eat whatever is available in their territory, with a large proportion of their diet being small mammals, and that they do not search specifically for saiga herds; thus, saiga calves in large aggregations are at a very low risk from wolves. $w_{t,A}$ is parameterised such that the probability of being killed by a predator in the first 6 days of life is 0.5 for a solitary calf and 0.03 for a calf in an aggregation of 10 000 saigas. The effects of varying q and W are explored in sensitivity analyses. The position of the calf in an aggregation is assumed not to affect predation risk; this assumption is less unrealistic for saigas than for other species because saigas gather in such large groups that the proportion of edge individuals is very low, and because individuals join aggregations over several days, so individuals do not remain at the edge throughout the period. Wolves are assumed not to exhibit a numerical response to calf numbers, in line with the available data.

3.3. Disease

An increase in disease risk is assumed to be a cost of aggregation. The probability of a calf dying from disease depends on the cumulative number of females arriving in an aggregation, including those that have since left. The risk of mortality from disease is assumed to be independent of age during the first 6 days of a calf's life. Because FMD is so infectious, all members of the aggregation can be assumed to have the same risk of exposure if any one individual is infected. All individuals are assumed equally likely to become infected through contact with livestock during their migration. The fact that FMD is highly infectious, and that infection is likely to be from an external source, means that either there is an epidemic, in which case all calves in the aggregation will be exposed, or there is not. Hence, females cannot influence the probability of exposure to FMD except through the one decision of whether to join an aggregation or not. The probability of death from disease is modelled using an exponential function:

$$d_t = d_0 e^{\beta F_t} \tag{4}$$

where: d_t = probability of a calf dying from disease in the aggregation on day *t;* d_0 = probability of a solitary calf dying from disease; F_t = cumulative relative aggregation size (total number of females that have joined the aggregation so far divided by maximum potential aggregation size, $N_{\max}$); β = rate of increase in disease risk with cumulative relative aggregation size.

The normalisation of the aggregation size by maximum potential aggregation size makes disease mortality density-dependent, on the assumption that the area covered by migrating and calving herds varies with herd size, and infectious livestock are uniformly distributed over the steppe. It is difficult to estimate the baseline probability of a solitary calf dying from FMD, because recent data are strongly influenced by policies affecting vaccination regimes and livestock densities in saiga range areas. The value used for d_0 represents a 50% chance of mortality in an outbreak, with outbreaks occuring every 40 years; a range of values are tested in the sensitivity analyses (Table 1).

3.4. Overall mortality rates

The probabilities of a calf dying from predation or disease are assumed to be independent, so that the overall probability of death from these two factors on a given day is:

$$m_{t,A} = w_{t,A} + d_t - w_{t,A} d_t. \tag{5}$$

A calf's overall probability of death, during the period when mortality is dependent on the female's decision-making, is calculated as:

$$M = 1 - \prod_{t=A=1}^{t=A=6} (1 - m_{t,A}) \tag{6}$$

for a calf born on the first day of the birth period; for subsequent days, *t* is increased relative to *A* as appropriate.

3.5. Female choice

The model is in the form of a deterministic dynamic game. Each day, the newly arrived females make a decision as to whether to join an existing aggregation, create a new aggregation or calve solitarily. This decision leads to the updating of the size of each aggregation as calves are added to the aggregations. It is assumed that all females make their decisions simultaneously each day, and all females giving birth on a particular day make the same decision. This is a reasonable assumption because females arrive together at the birth area in migrating herds rather than individually. Next, predation reduces aggregation size, and also alters age structure by preferentially removing younger animals. However, because mortality from FMD occurs in the form of an epidemic, rather than being due to endemic disease, it either causes a very high mortality or none. Thus, there is no removal of calves based on their probability of death due to disease.

The female's decision is based on minimising *M* (Eq. (6)), the overall probability of calf mortality over the 6 day period when the calf is vulnerable to predators (and hence when being in an aggregation is potentially beneficial). Calf mortality is assumed to be affected only by the number of calves within its own aggregation, implying that the size of the area where the saigas give birth is large enough that interactions between groups are negligible. The optimal decision for an individual female depends on the decisions made by the females calving both before and after her and on the number of females calving on each day (i.e. on the position of that female's calf in the distribution of birth dates).

The cohort of females arriving on a particular day has three options; join an existing aggregation, form a new aggregation or calve solitarily. Given that they choose to calve within an aggregation, there are four strategies available to each cohort; they can stay in their chosen aggregation for 3–6 days. If they leave the aggregation before the end of the period of neo-natal vulnerability (6 days), their calf's mortality rate from predation changes to that of a solitary calf as soon as they have left the aggregation. Their mortality rate from FMD changes to the solitary rate after a lag of one day, to reflect the observed FMD latent period of 24–48 h in saigas (Nagumanov, 1972).

The optimal strategy for a female giving birth on a particular date is determined as a 'game against the field'. Hence, the female is assumed to be making a decision in the context of of a given set of decisions made by the other females. In this case, it is assumed that each cohort of females (those that give birth on the same day) makes the same decision, and their strategy is influenced by the strategies of the females giving birth on all other days.

Let $M(s, \hat{s})$ be the expected mortality of a calf when its mother follows strategy s and all the other females follow strategy $\hat{s}$. A sufficient condition for $\hat{s}$ to be an evolutionarily stable strategy (ESS) is that $M(s, \hat{s}) > M(\hat{s}, \hat{s})$ for all $s \neq \hat{s}$ (Mangel and Clark, 1988; recalling that females are aiming to minimise M). As it is possible that $M(s, \hat{s}) = M(\hat{s}, \hat{s})$ for some $s \neq \hat{s}$, a further condition is needed that that $M(s, \hat{s}) > M(\hat{s}, \hat{s})$ when only a small proportion of the population is following strategy s. This means that strategy s cannot spread in a population following strategy $\hat{s}$. In the case of the saiga antelope, $\hat{s}$ is not a single strategy, but a strategy set, with one strategy for each of the days on which females give birth.

The ESS is found iteratively, starting by calculating M for each birth day when all females follow a given strategy $\hat{s}$ (e.g. that all females join a single aggregation and remain in it for 6 days). The strategy for females giving birth on day 1 (s) is then changed to each of the other options in turn, and the mortality of their calves calculated given that females giving birth on all other days continue to follow the strategy set $\hat{s}$. The strategy s that produces the lowest value for $M(s, \hat{s})$ is retained, and the strategy set $\hat{s}$ is altered accordingly. The procedure is repeated for each of the other birth days in turn. When the new strategy set $\hat{s}$ for all birth days is found, the strategy followed by females on day 1 is revisited, and the procedure is repeated until no change in strategy can improve the value of $M(s, \hat{s})$ for any female. The iterative technique has the danger that it can find local rather than global ESSs; this is guarded against by re-running the procedure using several different starting values for $\hat{s}$.

4. Results

The ESS under the baseline parameter values (Table 1) is shown in Fig. 3a, together with the associated overall probability of death. The females form a single aggregation, with those arriving first staying for the full 6 days, while later arrivals stay for shorter and shorter periods. Females arriving more than 10 days after the start of the birth period choose to remain solitary. The reason for this result is shown in Fig. 3b, which compares mortalities under the five unconditional strategies to that under the ESS; calves born late in the aggregation have a very high probability of death. This is chiefly because they are very vulnerable to predation when the herd size is relatively small, particularly because predators preferentially kill younger animals (Fig. 3c). It is interesting to note that the ESS does not have the lowest mortality rates for each arrival date; females arriving on days 6–9 have higher mortality rates under the ESS than under some of the unconditional strategies. This is because the females are optimising given the decisions made by other saigas; because those arriving from 10 days onwards choose not to join the herd, the protection from predation which their calves would have given to the earlier arrivals is not available.

Despite the fact that the ESS involves late arrivals not joining the aggregation, these females make up such a small proportion of the total number of saigas arriving in the birth area that the total herd size is little changed (Fig. 4). Thus, observation of saiga behaviour under the ESS

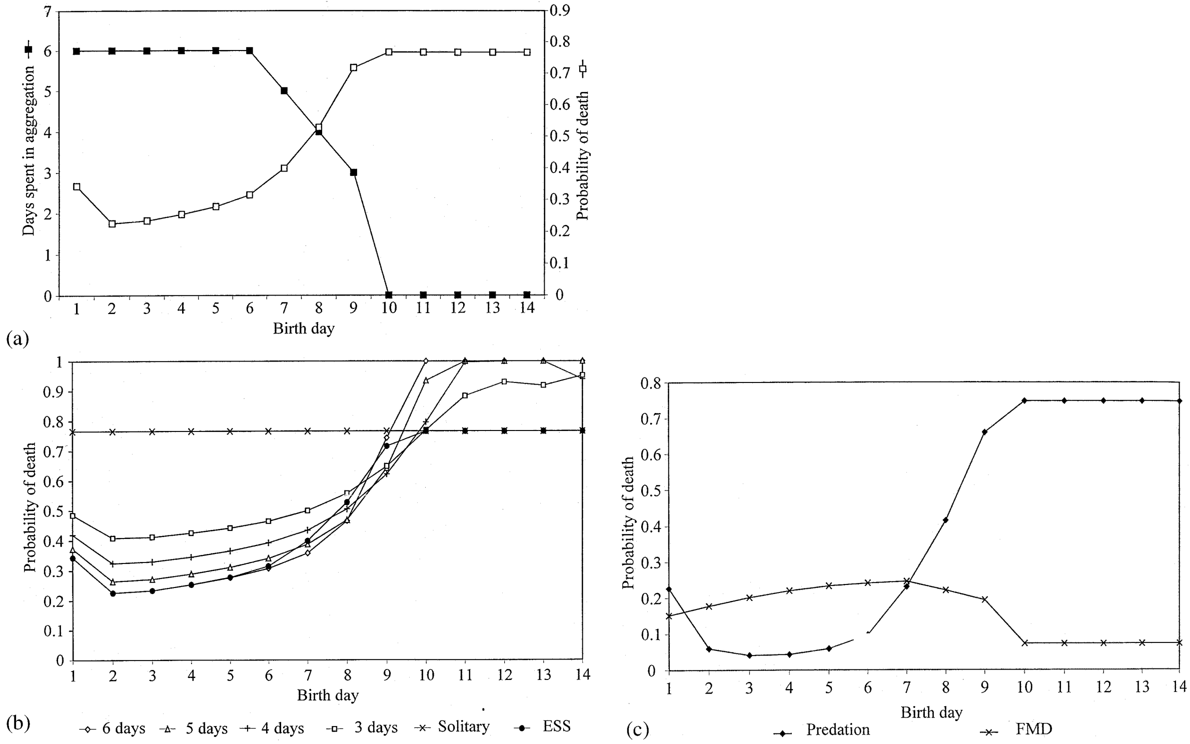

Fig. 3. (a) Evolutionarily Stable Strategy for the baseline parameter values shown in Table 1, and the probability of calf mortality under this strategy. The x-axis shows the day on which the calf is born, so the mortality rate is the overall probability for a calf born on that day, over the whole 6 days of the strategy. (b) Comparison of mortality rates under the ESS and under the five possible unconditional strategies (when all females follow the same strategy regardless of birth date). (c) Breakdown of mortality under the ESS into its component parts; the probability of being killed by a predator and the probability of dying from FMD.

would show 98.6% of saigas joining an aggregation, with only a very few late arrivals not doing so.

These results are generally stable to parameter variation. d_0 (the risk of a single calf dying of FMD) and q (the risk of a single calf being killed by a predator) were varied together over the range shown in Table 1. Varying the parameters together rather than singly leads to a more realistic senstivity analysis (Mangel, 1993). However, the changes in mortality rates caused by changes in these parameter values had only very minor effects on the ESS. As W (the total number of calves that can be killed by predators in a day) increases from 100 to 800, mortality rates within the aggregation increase, and the date on which female saigas chose to leave the aggregation changes from day 12 to 9 but the ESS otherwise remains the same as in Fig. 3a.

The variable that has the strongest effect on the ESS is the total number of saigas arriving in the birth area, N_{tot}. This changes not only the number of days females choose to remain in an aggregation but also the number of aggregations that are formed. Fig. 5a shows the ESS and Fig. 5b the associated mortality rates as N_{tot} varies from 5000 to the maximum of 100 000. At $N_{\text{tot}} \geq 70\,000$, the mortality rates drop in the first few days of the birth period. This is due to these cohorts of females choosing to form new aggregations rather than join existing aggregations, thus reducing their disease risk. This only happens among the females arriving in the first few days, because the numbers arriving on these days are large enough to keep predation rates low in the new aggregation. If $70\,000 \leq N_{\text{tot}} \leq 85\,000$, two aggregations are formed; if $N_{tot} \geq 90\,000$, three aggregations are formed (Fig. 5c).

One of the concerns that has been expressed about increased poaching is that disturbance during the mating season and very low proportions of males in the population may lead to an increase in the spread of birth dates and later average conception dates (Ginsberg and Milner-Gulland, 1994). I test the effects of this by changing the parameters of the Gamma distribution for births (Fig. 2). When births are less clumped, the base case ESS involves joining a single aggregation; no females choose to calve solitarily, although later arrivals still do leave the herd early (Fig. 6a). Mortality rates are lower than with the more peaked birth distribution except for the very first births. Although this result may suggest that strong temporal clustering is not advantageous for saigas, it must be remembered that we are are dealing only with the effects of spatial clustering in this model, on the assumption that temporal clustering is a response to climate and vegetation availability. The effects of changes in N_{tot} are less strong for the less peaked birth distribution; the ESS only changes markedly if $N_{tot} \leq 20\,000$, and two aggregations are only formed when $N_{tot} \geq 85\,000$ (Fig. 6b and c). Because the peak of births is later, the cohorts forming the new aggregation are those arriving on days 3–5, as opposed to those arriving on days 1–3 in the more peaked distribution.

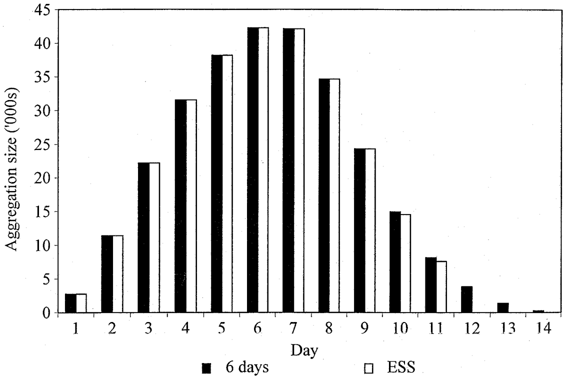

Fig. 4. Size of the aggregation each day when all females join the aggregation and stay for the maximum length of time ('6 days'), compared to the ESS aggregation size. Note the small difference between the two, despite the ESS involving females not staying in the aggregation for the maximum length of time from day 7 onwards.

There have been several impacts on the Betpak-dala saiga population accompanying the recent political changes. The effects of a combination of changes on model predictions can be very different to those of each single change. Thus, the model parameters were altered to reflect an increase in the population density of wolves because culling has stopped (increasing parameters q and W); a decrease in the saiga population size due to poaching (decreasing N_{tot}); possible changes in the spread of birth dates and the location of the peak birth date due to poachers targetting males and poaching during the mating season (changing a and c). The change in FMD risk is affected by two conflicting processes: a decrease in contact rates caused by a drop in livestock numbers, but an increase in the probability that a given contact is with an infected animal, caused by a reduction in routine vaccination. An increase in d_0 is modelled, assuming that the latter effect is dominant (because of the infectiousness of FMD). A realisation of this particular combination of changes in parameter values is shown in Fig. 7a; this is presented as an example only, as other values might produce very different conclusions. Mortality rates of calves born early in the birth period are much higher under the Betpak-dala combination of parameter values than in the base case; later, the mortality rates are more similar (Fig. 7b). The ESS is similar to the base case, but saigas tend to stay in the aggregation slightly longer at the end of the birth period, as protection against increased predation. The first arrivals also leave the aggregation early, reducing their FMD risk.

Whether or not such changes in behaviour would actually be observed in female saigas under the kind of stress currently being seen in Betpak-dala depends on how much of saiga behaviour is innate, and how much the females are able to adapt to changing circumstances. It seems unlikely that female behaviour could change in response to short-term changes in FMD risk. The most plausible cue for behavioural alteration is a change in the number of other females arriving at the birth area; thus, it is interesting that the model predicts that the ESS is rather sensitive to this

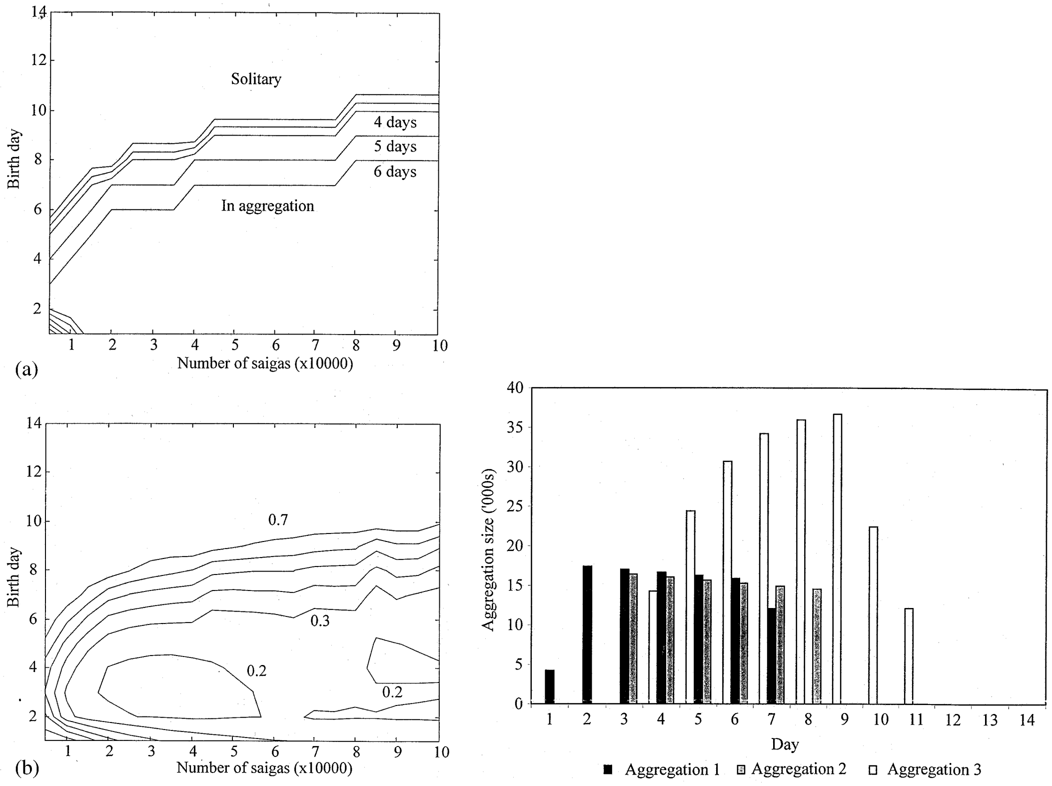

Fig. 5. (a) Effect of changes in the total number of saigas giving birth, N_{tot}, on the ESS for each birth day. The contours show the ESS. Hence, for the base case shown in Fig. 3a ($N_{\text{tot}} = 50\,000$), the ESS is to remain in the aggregation for the full 6 days if the calf is born on days 1–6 and to calve solitarily from day 10; the contours show the intermediate ESSs. The contour showing the option of remaining in the herd for 3 days is unlabelled in order to clarify presentation. (b) Effect of changes in the total number of saigas giving birth, N_{tot}, on the probability of calf mortality for each birth day. Contours show overall mortality rates at the ESS—contours for mortalities between 0.3 and 0.7 are unlabelled for clarity of presentation. The base case, shown in Fig. 3a, is at $N_{\text{tot}} = 50\,000$. The lower mortalities for birth days 1–3 at high values of N_{tot} are caused by individuals forming new aggregations rather than joining existing ones. (c) Example of changes in the size of aggregations over time for a realisation in which three aggregations are formed (where $N_{\text{tot}} = N_{\text{max}} = 75\,000$).

parameter. If all the females continued with the base ESS under Betpak-dala conditions, mortality rates would be rather similar in the first 6 days, and in the last few days (when the females are calving solitarily). Between days 7 and 10, mortality rates diverge, so that on day 10, the base ESS gives a mortality rate 24% higher than the Betpak-dala ESS (Fig. 7b). Thus, for the majority of the females (73% of them), following the base ESS is not severely suboptimal. It is interesting to note that although the Betpak-dala set of parameter values massively increases mortality rates over the base case early in the birth period, it is later in the birth period that following the base ESS is most sub-optimal.

5. Discussion

Little is known about the reproductive strategies of the saiga antelope, except from anecdotal observations. However, it is clear that human disturbance has the potential severely to disrupt saiga reproduction. It is important for saiga conservation that the ways in which this disruption could manifest itself, and its potental impacts on population dynamics, are explored. The model presented here incorporates the effects of predation and disease on saiga females' choice to join aggregations or calve solitarily. The model is deterministic; this is appropriate because the relationship between female behaviour and the key variables affecting the state of the system (total population size, temporal distribution of birth dates, and mortality rates from predation and disease) is essentially deterministic. A stochastic approach to the problem could allow female behaviour to alter if she detected an FMD epidemic within the aggregation; this is far more complex to model, and is not used here on the assumption that the highly infectious nature of FMD precludes effective avoidance once disease presence is detectable.

It is assumed that aggregation at the time of birth is a predator-swamping mechanism, but that it has a cost in terms of an increased disease risk. This is not the only assumption that could have been made, but given the evidence available, it is a reasonable one. The model has been parameterised using values from the literature, but it is not possible to parameterise the model wth confidence without a detailed field study. Instead, it can be used to make qualitative predictions that need to be tested in the field. These are that, in a relatively undisturbed population like Ustiurt:

- Calves born later in the birth season should leave the aggregation earlier than those born early in the season.

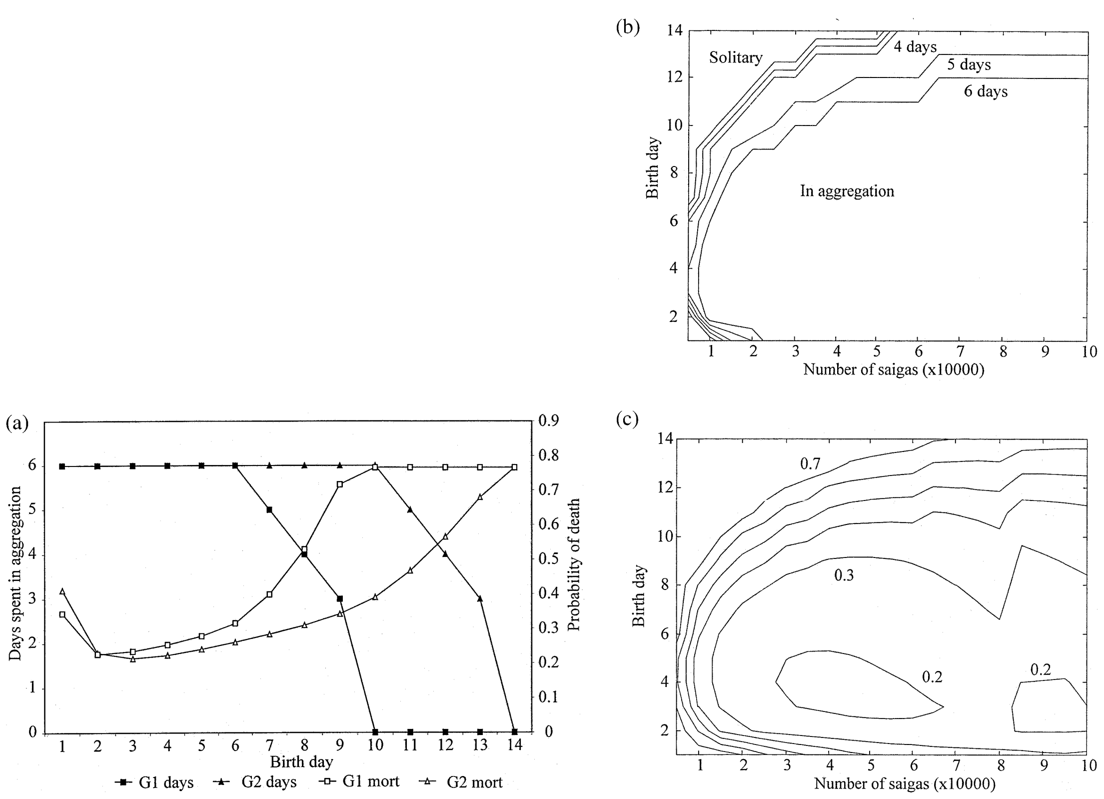

Fig. 6. (a) Comparison of the ESS ('days') and probability of calf mortality ('mort') under the two gamma distributions shown in Fig. 2; Gamma 1 ('G1') has $c = 4$, $a = 1$, Gamma 2 ('G2') has $c = 3$, $a = 2$. (b) Effect of changes in the total number of females giving birth, N_{tot}, on the ESS for each birth date under the Gamma 2 distribution. This should be compared to Fig. 5a. (c) Effect of changes in the total number of females giving birth, N_{tot}, on the probability of mortality for each birth date under the Gamma 2 distribution. This should be compared to Fig. 5b. The lower mortalities for birth days 3–6 at high values of N_{tot} are caused by individuals forming a new aggregation rather than joining the existing aggregation.

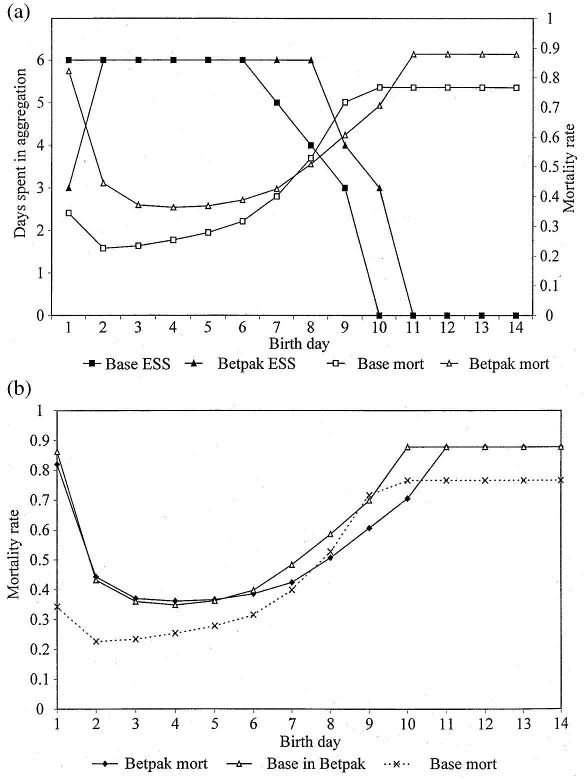

Fig. 7. (a) Comparison of the ESS and associated probability of calf mortality ('mort') under the base case ('Base', Table 1), and a set of parameter values representing the current situation in Betpak-dala ('Betpak'; parameter values as in Table 1 except that $N_{\mathrm{tot}} = 25\,000$, $W = 600$, $d_0 = 0.025$, $q = 0.66$). (b) Comparison of calf mortality rates under the Betpak-dala set of parameter values when the females follow the associated ESS (filled symbol) or continue to follow the base-case ESS (open symbol). Also shown for comparison (dashed line) is the probability of mortality when following the base-case ESS under the base-case parameter values.

- Very late arrivals do not join aggregations, but calve solitarily.
- The vast majority of saigas do join aggregations.
- Increases in predation risk cause saigas to leave aggregations earlier.
- Female behaviour is most sensitive to changes in the number of females arriving in an area.
- If a very large number of females arrives in an area, they will form more than one aggregation; these new aggregations are only formed in the first few days of the birth period.

Predictions about the effects that human disturbance has on female decision-making could be tested by comparing the Ustiurt population to the Betpak-dala population:

- If birth dates become more spread out, females tend not to calve solitarily so much. Fewer aggregations form, and more than one aggregation forms only at very high numbers. New aggregations form later in the birth period.
- The Betpak-dala saiga population currently has a much higher probability of calf mortality during the birth period, particularly among the early arrivals.
- The ESS does not change significantly under current Betpak-dala conditions. If the females can adapt to the new conditions, the aggregations would be expected to last a few days longer.
- Splitting into smaller aggregations under Betpak-dala conditions is not predicted by the model. This suggests that the smaller aggregations and greater dispersal of females observed in Betpak-dala are caused by disturbance during the birth period, rather than by changes in female behaviour.

The next step is to establish a research programme to address these predictions, collect data to parameterise the model better, and test the underlying hypotheses concerning the biological mechanisms that cause saigas to aggregate. The research should include comparative studies of female behaviour in aggregations of different size, because aggregation size is a key variable determining the ESS and is a cue to which females could respond. Quantitative data on calf mortality rates from predation are needed, together with systematic observation of female behaviour during the birth period. A full study of female reproductive behaviour would also include the rut; this would allow temporal clustering of births and dominance relationships to be investigated, as well as spatial clustering. For example, it might be that the dominant females would wish to give birth on days 2–4 of the birth period, when calf mortality rates are at their lowest.

Although these predictions are specific to the saiga antelope, the model also has more general applicability. Saigas provide an interesting case study of a species that forms temporary aggregations at the time of birth; the framework presented here would be directly relevant to other species with similar behaviour patterns, such as wildebeest (Estes, 1976). Aggregative behaviour in general has been shown experimentally to have both costs and benefits (Brown and Brown, 1986, 1987), but little modelling of the resultant trade-offs in individual decision-making has been carried out. Rubenstein (1978) modelled the trade-offs in a theoretical context, and Mangel and Clark (1988) concentrated on the costs and benefits of different foraging group sizes. In this paper, we model individual decision-making in the context of a trade-off between the two key factors commonly identified as influencing decisions that determine group size. This game-theoretic approach to the decision to join an aggregation is broadly applicable to many problems in the ecology of grouping behaviour.

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