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TRADE-OFFS IN MALE LEK BEHAVIOR

by

Sarah Alison Cowles

A THESIS

Presented to the Faculty of
The Graduate College at the University of Nebraska
In Partial Fulfilment of Requirements
For the Degree of Master of Science

Major: Biological Sciences

Under the Supervision of Professor Robert M. Gibson

Lincoln, Nebraska

December, 2013

TRADE-OFFS IN MALE LEK BEHAVIOR

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University of Nebraska, 2013

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In lek mating systems, males aggregate together and perform courtship displays to visiting females. However, display may be energetically expensive and reduce the time available for foraging. These costs in turn could lower energy reserves, which could decrease survival. I examined trade-offs in male lek behavior using two methods: 1) I conducted an empirical study of how sharp-tailed grouse (*Tympanuchus phasianellus*) males allocate time between courtship display (“dancing”), agonism, foraging, and inactivity in relation to female numbers both within and across days. I also measured head turning rates during these same behaviors as a proxy for visual attentiveness to the surroundings. 2) I created a stochastic-dynamic programming (SDP) model to investigate how the trade-off between reproductive success and survival (mediated by body condition) affects male reproductive strategies. In my empirical study, I found that the proportion of males engaged in display increased significantly with female numbers whereas foraging decreased significantly with female numbers both within and across days. This indicates that males increase display at the expense of reduced foraging time at periods of high female attendance. In addition, during display, males turned their head only half as frequently as during other activities, which suggests reduced visual attentiveness during display and the potential for increased predation risk. In the SDP

model, initial body condition largely determines the optimal seasonal breeding strategy. Males with initially lower body condition are predicted to forage early in the season, maintain lower condition throughout the season, and delay the onset of maximum display effort compared to males with initially higher condition. The results of the two studies suggest that male lek behavior is constrained by both the costs of display and the survival cost of maintaining body condition.

ACKNOWLEDGEMENTS

I would especially like to thank my adviser Dr. Robert Gibson for providing advice, resources, and support over the course of my time at UNL as a student in his lab. In addition, I would like to thank my committee members Dr. Brigitte Tenhumberg, Dr. Eileen Hebets, and Dr. Gwen Bachman for providing additional help and guidance. I would also like to thank SBS special funds for the funding necessary to support the field component of my M.S. project. Many thanks to Dr. Chad Brassil and Dr. Drew Tyre for statistical advice, the USFWS staff at VNWR for logistical support, the NGPC for capture permits, and the Nelson family of Valentine, NE for permission to use the Nelson lek site. I would like to thank Dr. Dai Shizuka, Dr. Nate Muchhala, Shivani Jadeja, and the graduate students in the scientific writing class for helpful comments during the writing process. Last, but certainly not least, I'd like to thank my parents Rich and Jackie for their unending support in my development as a scientist as well as the many other biology graduate students and post-docs at UNL for making science more enjoyable.

TABLE OF CONTENTS

CHAPTER 1: DISPLAYING TO FEMALES LOWERS MALE FORAGING TIME IN A LEKKING BIRD

Abstract.....	1
Introduction.....	2
Methods.....	6
Results.....	11
Discussion.....	14
References.....	18
Multimedia objects	
Figure 1.1: Within-day patterns of female numbers and male behavior.....	22
Figure 1.2: Across-day patterns of female numbers and male behavior.....	23
Figure 1.3: Head turning rates in different behaviors.....	24
Table 1.1: Repeated measures analyses of within-day male behavior in relation to female numbers and time.....	25

CHAPTER 2: HOW BODY CONDITION AFFECTS OPTIMAL BREEDING STRATEGIES ON THE LEK: A STOCHASTIC-DYNAMIC PROGRAMMING MODEL

Abstract.....	26
Introduction.....	27
Model Description.....	30
Results.....	39
Discussion.....	44

References.....	45
Multimedia objects	
Figure 2.1 The relationship between daily survival and body condition.....	54
Figure 2.2 The probabilities of gaining or keeping territories.....	55
Figure 2.3 Female attendance reproductive synchrony curves.....	56
Figure 2.4 The SDP optimal decision matrix.....	57
Figure 2.5 Baseline forward simulation model results.....	58
Figure 2.6 Population mean body condition simulation.....	59
Figure 2.7 Forward simulation results with different female synchrony curves..	60
Figure 2.8 Forward simulation results with increased on-lek predation risk.....	61
Figure 2.9 Territory status with increased on-lek predation risk.....	62
Figure 2.10 Male RS and survival with a reduced s_2 pay-off.....	63
Figure 2.11 Forward simulation results under the handicap scenarios.....	64
Table 2.1 Reproductive pay-offs, change in body condition, and eq. 2 parameters for each behavior choice in the SDP model.....	65
Table 2.2 Description of eight cohorts used in the forward simulation.....	65
Table 2.3 Costs and reproductive pay-offs in the handicap scenarios.....	65

CHAPTER 1: DISPLAYING TO FEMALES LOWERS MALE FORAGING TIME IN A LEKKING BIRD

ABSTRACT

Sharp-tailed grouse (*Tympanuchus phasianellus*) males attend leks and display to visiting females, but increased display may be energetically costly and reduce the time available for foraging. I used lek-wide scan sampling to study how males allocate time between courtship display (“dancing”), agonism, foraging, and inactivity in relation to female numbers both within and across days. I also videotaped 13 males and scored head turns during these different activities as a measure of visual attentiveness. I found that the proportion of males engaged in display increased significantly with female numbers both within and across days. Additionally, both within and across days foraging decreased with increasing female numbers. My results also suggest that agonism increases on days of high female attendance after females have left the lek. During display, males turned their head only half as frequently as during other activities. The data suggest two mechanisms by which display costs are potentially incurred: 1) a reduction in on-lek foraging time, and 2) possibly reduced visual attention to the surroundings.

INTRODUCTION

Courting males face trade-offs between attracting mates and the associated costs of display. Male courtship behavior is constrained by a wide variety of costs, which can include increased energy expenditure from physiologically demanding displays, reduced time allotted to foraging, and increased predation risk (reviewed in Magnhagen 1991; M. Andersson 1994). However, in lekking bird species the proximate mechanisms by which these costs arise are still not well understood.

In avian lek mating systems, males contribute no parental care and therefore mainly face the reproductive costs of courtship display associated with competing for and attracting mates (Wiley 1974; Emlen & Oring 1977; Höglund & Alatalo 1995). Males compete through differential lek attendance (endurance rivalry), aggressive interactions that determine territory ownership, and variation in display effort that influences female mate choice (Gibson & Bradbury 1985; Höglund & Lundberg 1987; McDonald 1989; Pruett-Jones & Pruett-Jones 1990; Alatalo et al. 1991; Gibson et al. 1991; Gratson 1993; Fiske et al. 1998; Rintamäki et al. 2001; Alonso et al. 2010). In addition, females assess males based upon variation in traits that remain relatively stable over the breeding season, including differences in acoustic display quality (Gibson et al. 1991), the size and color of sexual ornaments (Alatalo et al. 1996; Stein & Uy 2006; Siitari et al. 2007; Dakin & Montgomerie 2011, 2013), and territorial characteristics (Gibson et al. 1991; Gratson et al. 1991; Hovi et al. 1994; Kokko et al. 1999).

Several studies indicate that lekking male birds lose mass through the breeding season and are therefore not in energy balance (Beck & Braun 1978; Höglund et al. 1992; S. Andersson 1994; Lebigre et al. 2012). It is uncertain whether this is due to increased

energy expenditure (see Vehrencamp et al. 1989; Höglund et al. 1992), a reduction in food intake, or through a combination of the two. If food intake decreases, it could be attributed to a reduction in available foraging time off the lek (due to increased time spent on the lek). Additionally, in species that forage on- as well as off-lek, male foraging time might additionally be reduced by participation in display, male competition, or another reproductive behavior while on the lek.

Lekking birds may also face increased predation risk while on the lek (e.g. Hartzler 1974; Trail 1987; Gibson & Bachman 1991). Males may reduce time on the lek in response to increased predation risk (Käläs et al. 1995; Boyko et al. 2004), choose lek sites that reduce visibility to aerial predators (Aspbury & Gibson 2004), and form mixed-species leks to reduce individual predation risk (Gibson et al. 2002). Collectively, these observations implicate predation as an additional cost of lek display. However, the mechanisms by which lek display increases exposure to predators are not well studied. Several possible processes could be involved: 1) displaying males could be more conspicuous to predators, 2) males could have increased exposure to predation risk due to increased time on the lek when females visit, and 3) males could have decreased visual attention to the surroundings during courtship, as suggested by the limited attention hypothesis, or LAH (Dukas & Kamil 2000a, 2000b). The LAH posits that animals have limited cognitive attention and, when engaged in demanding visual tasks, individuals are less likely to notice peripheral targets such as an approaching predator (Dukas & Kamil 2000a, 2000b; Dukas 2002, 2004, 2009; Kaby & Lind 2003; Fernández-Juricic et al. 2004).

Evaluating changes in male behavior on the lek when females are present could help to identify some of the cost-incurring mechanisms mentioned previously. When females are present, males shift behavior towards courtship display (Wiley 1973; Höglund & Lundberg 1987; McDonald 1989; Pruett-Jones & Pruett-Jones 1990; Gratson 1993; Rintamäki et al. 2001; Nooker & Sandercock 2008), and may stay longer on the lek (e.g. Boyko et al. 2004). Examining compensatory shifts in other behaviors (such as foraging) could reveal temporal trade-offs by which the costs of display arise.

In addition, if male activities change with female presence, and visual attention levels change with different activities, then overall visual attention levels could vary with female presence. Although visual attention during different behaviors is difficult to measure in a non-laboratory setting, a possible way of evaluating LAH in the field would be to use head movements as a proxy measure of visual attention (Fernández-Juricic 2012). This is because birds rotate their heads either to track objects detected in the peripheral visual field on foveal areas of high receptor density or to scan the surroundings (Andrew & Dharmaretnam 1993; Land 1999; Dawkins 2002; Jones et al. 2007; Gall & Fernández-Juricic 2010).

I was interested in addressing the costs of display both through trade-offs with other behavioral activities and the LAH using sharp-tailed grouse (*Tympanuchus phasianellus*) males. On the lek, sharp-tail males are subjected to both aerial (raptor) and ground (coyote) predators (pers obs), which they detect visually (e.g. Evans et al. 1993). Lek size averages 9-10 males (Gibson et al. 2002). Males defend territories, and most territorial males are faithful to a single lek site for the spring breeding season (Kermott 1982). The breeding season lasts from late March to mid-May (Kermott 1982; Landel

1989). Each day, males arrive about 45 minutes before sunrise and stay on the lek up to 3 hours after sunrise (Kermott 1982), which is called the morning lekking period.

Throughout this period, sharp-tailed grouse males transition among various activities, including fighting with other males, sitting or standing, and courtship display “dancing.” Dancing includes an active dance phase with both visual (rapid movement and exposure of white undertail covert feathers) and acoustic (vocalizations and tail clicking) components, followed by an inactive pause phase where the bird holds the display posture but remains still. In contrast to many lekking species in which males do not obtain any benefits other than possible matings on the lek, sharp-tailed grouse allocate some time to foraging on forbs while on the lek arena (Gibson et al. 2002; pers obs.). The average mass of sharp-tail males declines through the spring breeding season (R. Gibson, unpublished data), which suggests sharp-tail males are not in energy balance during this time.

In this study, I investigated how sharp-tailed grouse males trade-off display with other behavioral activities on the lek in relation to changing female numbers both within and across days using time budget analysis. In addition, using head movements as a proxy measure of visual attentiveness, I explored the limited attention hypothesis in the field to see if sharp-tailed grouse males are potentially distracted during display.

METHODS

Study Site

I studied male sharp-tailed grouse lek behavior on and adjacent to the Valentine National Wildlife Refuge, in the Sandhills region of north-central Nebraska, USA. The refuge consists of alternating sand dune ridges and valleys covered by a mixture of prairie grassland and wetland habitats. I observed two different sharp-tailed grouse lek sites: the Nelson lek for 29 days between 5 April and 5 May 2011, and the West Twin Lake lek for 23 days between 10 April and 5 May 2012 (as the Nelson lek had only 4 males in 2012). All observations were made from first light to the end of the morning lekking period, up to three hours after sunrise, from an observation blind placed on the edge of the lek. I entered the blind in darkness before the birds arrived and stayed until they departed.

In each year, males were captured with walk-in funnel traps (Schroeder & Braun 1991) and were given a unique combination of three color bands and one metal band. In addition, to aid in individual identification during courtship display, I marked each captured bird's white under tail covert feathers with unique black pattern using a permanent marker. Seven of nine males captured in 2011 and four of six males captured in 2012 attended the study leks on a daily basis. During periods of data collection, maximum male daily counts were mean \pm SE = 8.72+0.18 on the Nelson lek and mean \pm SE = 15.09+0.61 on the West Twin Lake lek.

Daily and Seasonal Activity Budgets

To determine how male activity allocation varied with changes in female lek attendance, I conducted lek-wide scan samples on 20 days at the Nelson lek in 2011.

Sampling started as soon as all males were clearly visible and continued until the last male left the lek. However, for analysis I focused on a standard period from 10 minutes before to two hours after sunrise for which complete data were available on all 20 sample days. I recorded the total number of males and females present on the lek and the activity of each male present on the lek at 10-minute intervals, and later classified male activities into five separate categories: courtship display, foraging, agonistic behavior or agonism (fighting and face-offs—a form of agonistic behavior in which males sit and face each other, also called confronted crouching by Hjorth 1970), inactivity (sitting and standing), and “other” behaviors (preening, walking, and running). For each 10-minute interval, I then calculated the proportions of males in each behavioral category. The category of courtship display broadly consisted of males in dancing and pause phases, flutter jumps, and cooing (display vocalizations); however, this category mainly consisted of males in dancing and pause phases, as there was a high positive correlation between the proportions of males in the broad category of courtship display (mean \pm SE = 0.15+0.01) and the proportions of males only in dancing and pause phases (mean \pm SE = 0.11+0.01; Pearson correlation: $r = 0.94$, $N = 407$, $P < 0.0001$).

Head Turning Rates

To examine differences in head turning rates between different behavioral categories, focal videos of sharp-tail males in each of the four most common behaviors: courtship display (only dancing and pause phases), foraging, face-offs (a form of agonistic behavior), and inactivity (sitting and standing) were collected opportunistically throughout the morning lekking period. I videotaped seven color-banded males at the

Nelson lek in 2011 and six males at the West Twin Lake lek in 2012. Two of the six males recorded in 2012 were unbanded, but they were stable territory holders and were bordered by banded territory neighbors. I videotaped males at 30 frames/sec in AVCHD format using a Panasonic Lumix DMC-GH2 camera and a 100-300mm Panasonic zoom lens.

Video was collated by activity using the video software program Adobe Premiere Elements 9 (Adobe Systems, Inc.: San Jose, CA, USA). The mean video times recorded for the seven males in 2011 were (reported as mean \pm SE): display: 2.2+0.4 min, foraging: 4.2+0.7 min, agonism: 8.0+1.5 min, and inactivity: 7.3+1.2 min. In 2012, the mean video times for the six males were: display: 3.0+0.3 min, foraging: 3.7+0.5 min, agonism: 6.0+0.6 min, and inactivity: 5.5+0.8 min. I scored head turns for males in each behavioral category. Only right-left rotational head turns in the horizontal plane were scored. These turns were discarded if the head rotation was followed by a body turn (i.e. birds also turn their heads when changing direction). This method also discounts the normal forward head-bobbing motion of walking birds (compensatory head movements: Dunlap & Mowrer 1930) but includes rotations in the vertical plane (i.e. looking at the sky) that always involved a rotational component in the horizontal plane. I also discarded any up-down head movements during foraging, as these were assumed to be associated with food-searching. This makes my estimate of head turns during foraging a conservative estimate of visual attention. In preliminary analyses, I found no difference in head turning rates between the dancing and pause phases of courtship display (Paired t-test: $t_{12} = 1.13$, $P = 0.28$) and therefore combined dancing and pause phases when calculating the head turning rate for display.

Data Analyses

I analyzed the relationship between female numbers and male activity allocation at two temporal scales. First, I examined variation between scans within days from 10 minutes before to two hours after sunrise using repeated measures models (SAS Proc mixed, version 8.0). In these models, I used Julian day as the repeated measure and the number of females present on the lek and time of day as explanatory variables to investigate relationships with the proportions of males in display, foraging, agonism, and inactivity on a daily time scale. All reported p-values are based on t-statistics. Analyses using female numbers omit five days with no females. Because numbers and identities of males on the lek remained relatively stable over the sampling period, female- and time-related variation in male activities is unlikely to be due to changes in lek composition.

I also analyzed covariation between female numbers and male time allocation across days. I first averaged the proportion of males in each behavioral category across 10-minute interval within days to give a single proportion per day for each behavioral category. I then used GLMs in R version 2.11.1 (R Development Core Team 2010) to examine relationships between the maximum female daily count and the proportions of males in display, foraging, agonistic behavior, and inactivity on a seasonal time scale. In addition, I also examined models with both the maximum female count and date as explanatory variables to examine seasonal changes in behavior. All reported p-values are based on t-statistics and $df = 19$ for all models. The daily mean number of males per scan (mean male number) did not change with day in season (mean \pm SE = 0.02 ± 0.02 , $t_{18} = 0.84$, $P = 0.41$). I also included daily mean male number as a covariate with female

numbers in the models to check that variation in male numbers across days did not confound the patterns already identified with female numbers.

To analyze differences in head turning rates, I used random effect generalized linear mixed models (GLMMs) in the nlme package in R version 2.11.1 (R Development Core Team 2010).

RESULTS

The effect of females on male activity

Across days, the total time males spent on the lek during the morning lekking period did not increase significantly with maximum female numbers (mean \pm SE = 1.24 ± 2.8 , $t_{21} = 0.44$, $P = 0.662$). Subsequent analysis therefore focuses on male time allocation.

Within the morning display period, the mean proportions of males engaged in the four main activities were (mean \pm SE): display: (0.165 ± 0.016), foraging: (0.173 ± 0.026), agonism: (0.336 ± 0.025) and inactivity (0.290 ± 0.020). The proportions of males engaged in display, foraging, and agonism, but not inactivity, varied with numbers of females on the lek (Table 1.1). Male display significantly increased with female numbers, whereas both agonism and foraging decreased (Table 1.1). However, the proportion of males displaying also declined through the morning whereas agonism and foraging increased, coincident with decreasing female numbers (Figure 1.1, Table 1.1). To separate the effects of female numbers and time of day I ran GLMs with both time and female numbers as predictors of each activity. After controlling for time of day, display increased with female numbers while agonism and foraging decreased with female numbers as before (Table 1.1). Additionally, after controlling for female numbers display decreased whereas foraging increased with time of day.

Across days, the mean proportion of males engaged in display increased significantly with female numbers (mean \pm SE = 0.022 ± 0.006 , $P = 0.002$), whereas the proportion of males engaged in foraging behavior significantly decreased (mean \pm SE = -0.027 ± 0.011 , $P = 0.026$), and inactivity showed a non-significant negative relationship

(mean \pm SE = $-0.011+0.01$, $P = 0.27$). Unlike the within day pattern, however, across days agonism did not decrease with increasing female numbers (mean \pm SE = $0.019+0.011$, $P = 0.11$) (Figure 1.2). With date added to the models, the proportion of males engaged in display showed a non-significant negative trend with date (mean \pm SE = $-0.003+0.001$, $P = 0.08$), the proportion of males engaged in foraging significantly decreased with date (mean \pm SE = $-0.007+0.002$, $P = 0.005$), and the proportion of inactive males did not change with date (mean \pm SE = $0.003+0.002$, $P = 0.15$). In these three previous models the patterns with female numbers did not change. However, with date in the model, the proportion of males in agonism increased significantly with female numbers (mean \pm SE = $0.022+0.009$, $P = 0.03$) and increased significantly through the season (mean \pm SE = $0.007+0.002$, $P = 0.004$).

Further analysis suggests that the discrepancy between the effects of female numbers on male agonism within and across days is explained by variation in the temporal distribution of male activity throughout the morning. A reduction in agonism when females are on the lek (within days), but no reduction on days when more females attend (above) suggests that in the latter context agonism might have increased later in the morning after females had left. To investigate this possibility, I split days into “low” (0-1 females, 9 days) and “high” (2-7 females, 12 days) female attendance categories and tested for an interaction between time of day and attendance category. There was a significant interaction between the effects of female attendance category and time of day on the proportion of males engaged in agonism (mean \pm SE = $0.0021+0.0007$ min, $P = 0.0022$). Agonistic behavior increased through the morning on high female attendance days (mean \pm SE = $0.0021+0.0005$ min, $P < 0.0001$), but not on low female attendance

days (mean \pm SE = -0.00005 ± 0.0005 min, $P = 0.92$). None of the other behaviors showed a significant interaction between female attendance category and time of day.

Head Turning Rates

Head turning rates differed significantly among the four behavioral categories of display, foraging, agonism, and inactivity ($F_{3,36} = 18.43$, $P < 0.0001$) using a random-intercept GLMM with behavioral category as a fixed effect and bird nested within year as a random effect. This model was a better fit than a model with the same fixed effect but a random effect of bird only (Likelihood ratio test: $G = 10.24$, $P = 0.0014$). Since the model including year in the random effect was a better fit to the data, I can conclude there was a difference in head turning rates between the two years, with higher head turning rates across all behaviors at the lek studied in 2012 (mean \pm SE = 24.8 ± 2.0 turns/min) than in 2011 (mean \pm SE = 15.8 ± 1.2 turns/min). Using post-hoc Tukey HSD tests, the rate of head turning during display was significantly lower than during the other three activities ($Z > 5.167$, SE = 2.118, $P < 0.001$), which did not differ from each other (see Fig. 1.3). This pattern is consistent with the hypothesis that displaying males may be less visually attentive to their surroundings.

DISCUSSION

I found that male sharp-tailed grouse allocate more time to display with increasing female numbers at the expense of foraging both within and across days. In addition, I examined head movement rates in different activities and found that males turn their head only half as much during display compared to during other behaviors. This suggests two mechanisms by which display costs may be incurred: 1) a reduction in foraging time, and 2) possibly reduced visual attention to the surroundings.

Although lek-wide activity data provides information about overall trade-offs faced by displaying males, it is limited in that it doesn't provide information about individual variation between males. Nonetheless, my results show that foraging on the lek declines whereas display increases with female numbers both within and across days. These patterns remained robust when controlling for time both within mornings and across days. As far as I know, this is the first demonstration of a foraging-display trade-off in response to female attendance in a lekking bird. This trade-off suggests that time spent foraging likely decreases during peak periods of female attendance and that reduced food intake may be a cost of increased display. However, this inference assumes that males do not engage in compensatory foraging after leaving the lek. While off-lek foraging has not yet been studied, sharp-tail males may return to the lek multiple times each day during the seasonal peak in female lek attendance (R. Gibson, unpublished data) which suggests that time for compensatory foraging may be limited.

The ability to compensate for reduced foraging and/or increased energy expenditure may depend on territorial/reproductive status, and is possibly species-specific. For example, compensatory foraging is suggested to occur in sage grouse, in

which Vehrencamp et al. (1989) found that a subset of males that showed high energy expenditure (presumably due to increased display) actually lost less weight per day compared to males that showed lower energy expenditure. In lekking black grouse, reproductively successful males lost more mass over the breeding season than less reproductively successful males (Lebigre et al. 2012). This pattern may reflect the energetic cost of increased rates of agonistic interaction experienced by centrally-located, reproductively successful males (Rintamäki et al. 2001).

In addition, changes in male foraging behavior or the ability to compensate for increased energy expenditure during the breeding season may be affected by local food availability. For example, western capercaillie males may reduce the quality of their diets during the lekking season by feeding on higher quantities of nutrient-poor pine needles because these take less effort to find near the lek compared to richer nutrient sources (Odden et al. 2003). In several species of lekking manakins, lek sites may have higher food availability than more distant foraging locations (Ryder et al. 2006), which may offer males increased foraging opportunities without leaving the lek.

I also found that the reasons why foraging declines with increasing female numbers within days differ from the reasons behind the across day pattern. Within days, sharp-tail males increase display at the expense of reduced foraging and agonism when female numbers increase. However, with increased female numbers across days, males increase display at the expense of foraging, but agonism instead increases with females. My results suggest that males increase agonism later in the morning after the females have left on days with higher female numbers. Nooker and Sandercock (2008) found both display and aggression levels were higher when females were present on the lek in the

congeneric Greater prairie chicken (*Tympanuchus cupido*). In addition, they found that mating success was higher if males allotted more time to aggressive behavior compared to display behavior when females were not present on the lek.

In the second part of the study, I found that sharp-tailed grouse males turn their heads only half as frequently during display (Fig. 1.3) as during foraging, agonism, or inactivity. Assuming that head movements reveal visual attentiveness (see Introduction), this result could indicate that displaying males are less visually attentive to their surroundings (the limited attention hypothesis). If so, males might be more vulnerable to predation during display. A possible alternative hypothesis is that a static head during display serves some display-specific function, and therefore does not necessarily indicate lowered visual attentiveness. An experimental approach measuring head movements in response to a controllable visual stimulus (as a distractibility measure) in different behavioral contexts would be necessary to critically evaluate the limited attention hypothesis.

I also found higher overall head turning rates in 2012 than in 2011. The lek studied in 2012 was larger than in 2011, and since individuals may change their head position to monitor other conspecifics (e.g. Fernández-Juricic et al. 2005), a larger lek size in 2012 might account for higher overall head turning rates that year. Because sharp-tail males consistently defend territory boundaries from neighboring birds, they need to observe conspecifics and may turn their heads to do so.

To summarize, lekking male sharp-tailed grouse increased display at the expense of on-lek foraging with increasing female numbers both within and across days. In addition, males turned their heads less frequently during courtship display, possibly

indicating reduced visual attentiveness and therefore potentially increased vulnerability to predation. These two potential costs of courtship display could be further explored by studies that (i) investigate the effect of increased lek display on overall food intake, and (ii) experimentally probe the visual attentiveness of males engaged in display versus other activities.

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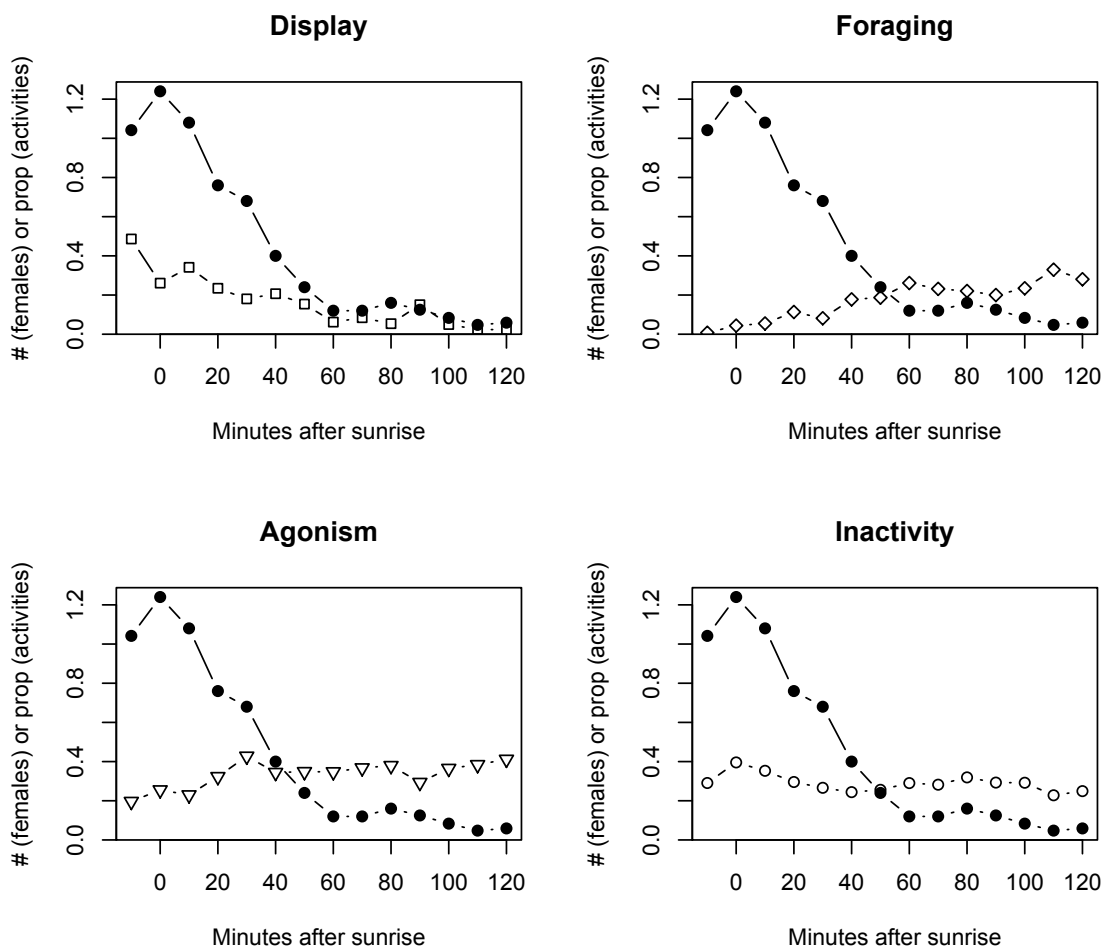


Figure 1.1: Mean within-day temporal profiles of female attendance (closed circles) and proportions of males engaged in each of four major behavioral categories: display (open squares), foraging (diamonds), agonism (triangles), and inactivity (open circles). See Table 1 and text for statistical analysis.

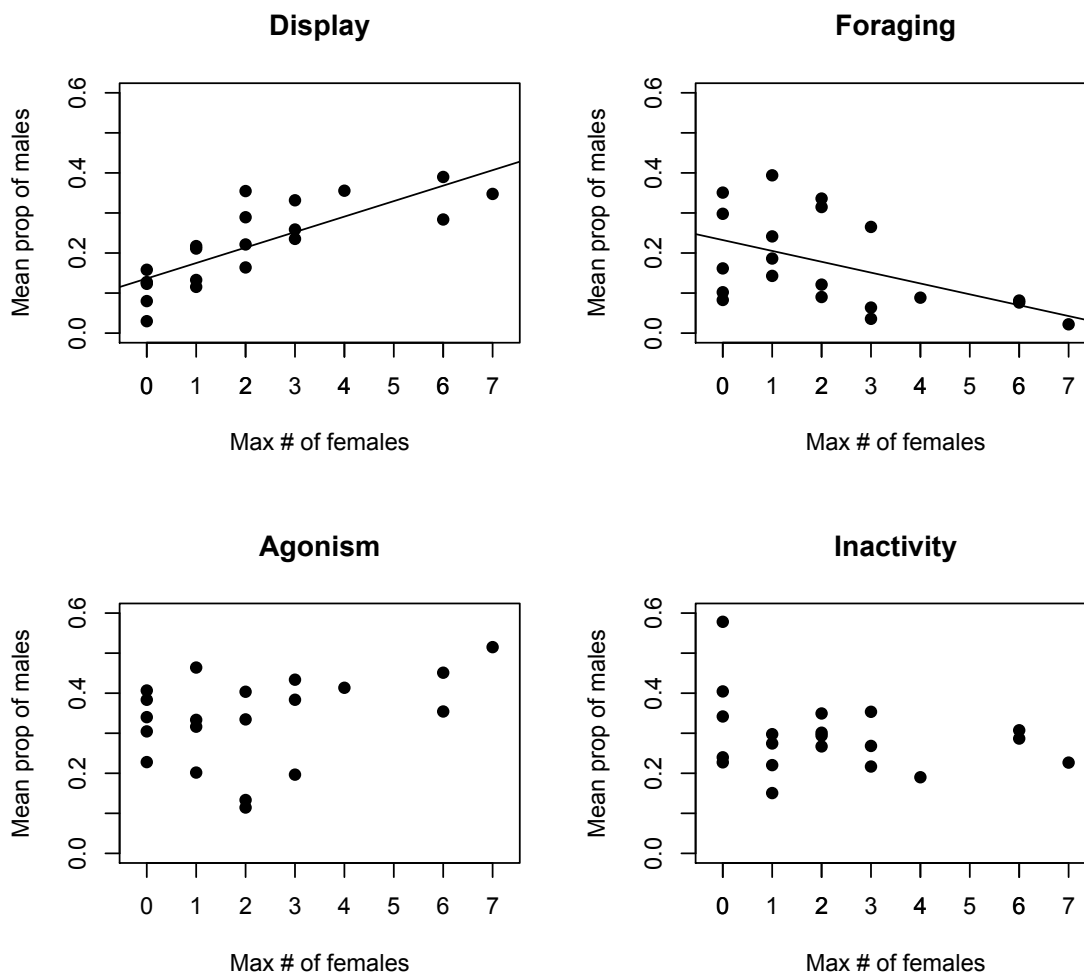


Figure 1.2: Mean proportions of male sharp-tailed grouse engaged in the four behavioral categories during the morning lek vs. maximum female daily count. See Table 2 and text for statistical analysis.

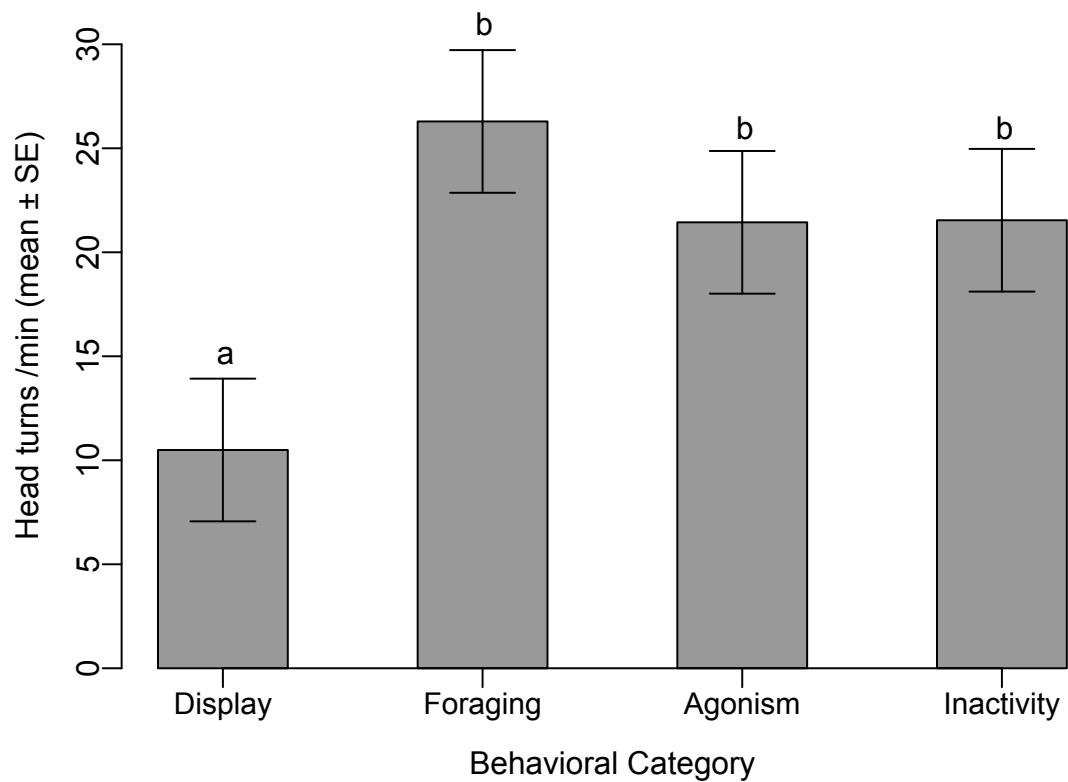


Figure 1.3: Head turning rates during each of four behavioral categories for 13 male sharp-tailed grouse. Letters above each bar indicate statistically homogeneous groups (Tukey tests, details in text).

Table 1.1 Repeated measures analyses of the effects of female numbers and time (minutes after sunrise) on the proportions of male sharp-tailed grouse in each of four behavioral categories within days. Panel A (upper) shows bivariate relationships and Panel B (lower) shows partial effects in models including both female numbers and time. P-values are based on t-tests.

Panel A				
Behavior	Females		Time	
	slope (SE)	P	slope (SE)	P
Display	0.163 (0.032)	0.0002	-0.003(0.0003)	<0.0001
Foraging	-0.052(0.012)	0.0009	0.002(0.0005)	0.0003
Agonism	-0.068(0.018)	0.0022	0.001(0.0005)	0.0262
Inactivity	0.013(0.023)	0.5824	-0.001(0.0004)	0.1563
Panel B				
Behavior	Females		Time	
	slope(SE)	P	slope(SE)	P
Display	0.128(0.03)	0.0009	-0.002(0.0003)	<0.0001
Foraging	-0.031(0.01)	0.009	0.002(0.0005)	0.0014
Agonism	-0.05(0.016)	0.0073	0.001(0.0005)	0.1441

CHAPTER 2: HOW BODY CONDITION AFFECTS OPTIMAL BREEDING STRATEGIES ON THE LEK: A STOCHASTIC-DYNAMIC PROGRAMMING MODEL

ABSTRACT:

Lekking males spend considerable time in courtship display, which may influence their energy budget through increased energy expenditure and reduced foraging time. This in turn could lower energy reserves, which may decrease survival. I built a stochastic-dynamic programming (SDP) model to investigate the trade-off between reproductive success and survival mediated by body condition (energy reserves). In my model males have three behavioral choices: 1) forage off the lek and gain body condition, but risk losing their lek territory, 2) engage in low-intensity display, which provides a low reproductive payoff but does not affect body condition, and 3) engage in vigorous, energetically costly display, which increases the chance to gain a territory and provides a high reproductive payoff but depletes body condition. My results suggest that body condition largely determines the optimal seasonal breeding strategy. Males with initially lower body condition are predicted to forage early in the season, maintain lower condition throughout the season, and delay the onset of maximum display effort compared to males with initially higher condition. In addition, female attendance synchrony and changes in the costs or relative payoffs of display alter the optimal behavioral sequence used throughout the breeding season. Under increased predation risk on the lek, males show higher reproductive success but decreased survival as initial body condition increases.

INTRODUCTION

In polygynous mating systems, males compete for access to breeding females (M. Andersson 1994). As a result, males invest time in reproductive behaviors such as aggression, fighting for dominance and/or territories with other males, and displaying to potential mates during the breeding season. However, time invested in reproductive activities during the breeding season can be energetically costly (Vehrencamp et al. 1989; Höglund et al. 1992; Lucas & Howard 1995; Lucas et al. 1996; McCauley et al. 2000; Isvaran & St. Mary 2003), and may also cause a reduction in foraging time or foraging on lower-quality food (Cowles, M.S. Chapter 1; Isvaran & Jhala 2000; Odden et al. 2003; Pelletier et al. 2006). As a result, males in many polygynous species lose mass over the course of the breeding season (*birds*: Beck & Braun 1978; Höglund et al. 1992; S. Andersson 1994; Lebigre et al. 2012; *flying fox*: Welbergen 2011; *frogs*: Wells 1978; *garter snakes*: Shine & Mason 2005; *pinnipeds*: Boyd & Duck 1991; Deutsch et al. 1990; Crocker et al. 2012; *ungulates*: McElligott et al. 2003; Barboza et al. 2004; Forsyth et al. 2005). Reduced energy reserves are associated with decreased survival (e.g. Ringsby et al. 1998; Christensen 1999; Hall et al. 2001; Harding et al. 2011). Thus, the energetic cost of reproductive effort is one mechanism that can generate a trade-off between reproduction and survival (see Williams 1966; Bell 1980; Martin 1995; Wingfield & Sapolsky 2003).

In polygynous systems, variation in energy reserves can affect male investment in reproductive activities and ultimately influence reproductive success. For example, males with larger fat reserves or mass at the beginning of the breeding season can have a longer breeding period (Gibson & Guinness 1980; Lidgard et al. 2005; Shine & Mason 2005).

Courtship behavior may also be affected, as males with more energy reserves may spend more time on courtship behavior (Mainguy & Côté 2008) and may be able to better afford energetically expensive courtship behaviors (e.g. Yuval et al. 1998). Higher rates and/or quality of courtship display in turn may increase mating success due to female mate choice (M. Andersson 1994). Finally, males with greater energy reserves may outcompete other males for territories or mates (e.g. Marden & Wagge 1990; Marden & Rollins 1994; Plaistow & Siva-Jothy 1996; Kervinen et al. 2012).

Despite empirical evidence that variation in energy reserves may play an important role in determining a male's reproductive success, there has been little systematic study of how variation in individual energy reserves influences male reproductive behavior throughout the entire duration of a breeding season. Exceptions are theoretical models of frog chorus dynamics by Lucas & Howard (1995), Lucas et al. (1996), McCauley et al. (2000) and of lek formation by Isvaran & St. Mary (2003). These models use the stochastic-dynamic programming (SDP) method in which the energy reserve of males is one of several factors determining the best reproductive strategy. The SDP method is a modeling approach used to predict the optimal series of behavioral decisions individuals must make through time to maximize their reproductive fitness based on initial assigned states (McNamara & Houston 1986; Mangel & Clark 1988; Houston & McNamara 1999; Clark & Mangel 2000).

Here, I develop a SDP model based on the biology of a seasonally breeding lekking bird to examine how an individual male's energy reserves affect reproductive tactics, reproductive success, and survival. During the breeding season, lekking males gather on an arena to compete for and defend display territories as well as to perform

displays to attract and court visiting females. Females choose a mate and copulate at the lek; males contribute no parental care (Höglund & Alatalo 1995). Male mating success in lekking birds is affected by the time males spend at the lek (lek attendance), territorial status, and display effort (Gibson & Bradbury 1985; Höglund & Lundberg 1987; McDonald 1989; Pruett-Jones & Pruett-Jones 1990; Alatalo et al. 1991; Gibson et al. 1991; Gratson 1993; Fiske et al. 1998; Rintamäki et al. 2001; Alonso et al. 2010). Additionally, variation in male attractiveness to females has been linked to characteristics that remain relatively stable over the breeding season, including differences in acoustic display quality (Gibson et al. 1991), the size and color of sexual ornaments (Alatalo et al. 1996; Stein & Uy 2006; Siitari et al. 2007; Dakin & Montgomerie 2011, 2013), and territorial characteristics (Gibson et al. 1991; Gratson et al. 1991; Hovi et al. 1994; Kokko et al. 1999).

My model investigates how lekking males should allocate their display effort through the breeding season in relation to initial body condition (defined as endogenous energy reserves at the beginning of the breeding season), territory ownership, and attractiveness level.

THE MODEL

The Baseline Model

I assume that males behave so as to maximize their lifetime reproductive success, in which case an optimization model can be used to predict their “optimal” behavior. Because lekking males mate polygynously and do not contribute parental care, variation in male reproductive success will be a function of variation in numbers of matings. Consequently I use male mating success as a proxy for lifetime reproductive success. I used a stochastic-dynamic programming (SDP) approach to examine the trade-off between male reproductive success and survival mediated by body condition in a model based on the biology of lek-breeding grouse. The model considers daily time steps. Each day males can choose between three behaviors: 1) stay off the lek and forage ($s1$), 2) attend the lek and engage in low-intensity display ($s2$), or 3) attend the lek and engage in high-intensity, energetically costly display ($s3$). A male must attend the lek and own a territory to mate, because females only mate with territorial males on the lek. High-intensity display increases the probability of gaining or maintaining a territory. For territorial males, high intensity display also increases the probability of mating with a female compared to low-intensity display. However, high intensity display decreases energy reserves (body condition), whereas reserves are unaffected by low intensity display. Males can only increase their energy reserves while foraging off the lek. Energy reserves affect survival as described below. Males foraging off the lek may lose their territory, and this risk increases the more time a male spends off the lek.

The SDP includes four state variables: time in the season, lek attendance, territory status, and body condition.

(1) Time in season, t : The model examines two 30-day long mating seasons, which would be applicable to bird species like the sharp-tailed grouse. $T = 60$ is the final time step at the end of the second breeding season. Since SDP models typically stabilize quickly, I would expect that the behavior of longer-lived males (i.e., males that live more than two seasons) would match the behavior in the first season for younger males and the behavior in the final season for older males.

(2) Lek attendance, l : A male is either off the lek ($l = 0$) or on the lek ($l = 1$).

(3) Territory status, r : A male may not own a territory or own a territory ($r = 0$ or 1 , respectively).

(4) Body condition, c : The body condition of a male is a measure of his energy reserves and varies between 0 and 42. We assume that body condition determines survival, λ , as specified below and illustrated in Fig 2.1.

$$\lambda(c) = \begin{cases} 0 & \text{if } c = 0 \\ \frac{1}{1 + e^{-6(c-10)}} & \text{if } 1 \leq c \leq 30 \\ 1 - \frac{c^4}{0.8c^5} & \text{if } c > 30 \end{cases} \quad (1)$$

Survival begins to decline below body condition state 18 and birds die of starvation if body condition drops to 0. Body condition state 30 is associated with maximum survival. If body condition is above 30, survival decreases because heavier birds may face higher predation risk (Gentle & Gosler 2001; Dietz et al. 2007; MacLeod et al. 2008).

Males that forage off the lek following $s1$ for a single time step gain one body condition unit for the next time step. Males that attend the lek and engage in low-intensity display for a single time step are assumed to be in energy balance and therefore do not change body condition for the next time step. Finally, males that engage in high-intensity display on the lek following $s3$ are assumed to expend large amounts of energy and lose two body condition units for the next time step.

Body condition, territory status, and display behavior, d , determine the chances of on-lek males gaining or losing a territory ($\text{Prob}\{r_{(t+1)} = 1 | r_{(t)} = 0\}$, or $\text{Prob}\{r_{(t+1)} = 0 | r_{(t)} = 1\}$, respectively, Fig 2.2). Values of parameters a and b were chosen to ensure the following conditions. First, a male following $s3$ is more likely to gain or keep his territory than a male following $s2$. Second, a male is more likely to keep a territory if he has one than gain a territory if he does not own one. Finally, the better condition a male is in, the more likely he is to gain or keep his territory (see Table 2.1 for parameter a and b values):

$$\beta(c, r, d) = \left\{ \frac{1}{a} \left(\frac{1}{1 + e^{-15(c+b)}} \right) \right. \quad (2)$$

A male foraging off-lek loses his territory with probability $\alpha(c) = 0.1$.

Between seasons: I assume that a male that survives the winter is able to replenish his energy reserves ($t = 30$ to $t = 31$). Thus, body condition at time step 31 is drawn from a truncated normal distribution (Mean = 30, SD = 6) that is capped within two standard deviations above and below the mean (i.e., within the range $c = 18-42$). For short-lived lekking bird species like sharp-tailed grouse, between-season survival is relatively low (Kermott 1982; Landel 1989). In my model, I set between-season survival (from $t = 30$ to $t = 31$) to 40% of the daily survival probability (at $t = 30$), $\lambda_{t=31}(c) = 0.4\lambda_{t=30}(c)$. Assuming that surviving territorial males have a high probability of maintaining a territory from year to year, a male's territory status at time $t = 31$ is the same as the territory status at $t = 30$ with a probability of $\delta = 0.8$.

At each time step, a male may accumulate a reproductive mating payoff which depends on his behavior, whether he owns a territory, his attractiveness, and female lek attendance. For simplicity, the model considers two levels of attractiveness (attractive or unattractive), which cannot change throughout a male's lifetime. I assume that female lek attendance changes throughout the season. In the baseline model, I use a "moderate reproductive synchrony" female attendance function f where the probability of a female attending a lek varies between 0.4 and 0.7 (equation 2, Fig 2.3). At each time step, the female attendance function f provides the probability that a male will mate and increase his fitness during that day (reproductive pay-off) if he owns a territory and is on the lek.

$$f(t) = \begin{cases} 0.4 + 0.02t & \text{if } 1 \leq t \leq 15 \\ 0.7 & \text{if } 15 \leq t \leq 24 \\ 0.7 - 0.06t & \text{if } 24 \leq t \leq 30 \end{cases} \quad (3)$$

I solved the SDP using the backward induction method (McNamara & Houston 1986, Mangel & Clark 1988; Houston & McNamara 1999; Clark & Mangel 2000). The algorithm starts at the final time step ($T = 60$) and works backwards through time. Male future fitness at $T = 60$ is set to zero because in my model males do not survive beyond two mating seasons. At each time step, the SDP determines for all possible combination of states the behavior that maximizes the lifetime fitness for attractive and unattractive males by using the following dynamic programming equation

$$F[l, r, c, t, T] = \lambda(c) * \max(s1, s2, s3) \quad (4)$$

with

$$s1 = [\alpha(c) * F[0, z(r-1), c+1, t+1] + (1-\alpha(c)) * F[0, r, c+1, t+1]]$$

$$s2 = [\beta(c) * (F[1, z(r-1), c, t+1] + w(R_L)) + (1-\beta(c)) * (F[1, r, c, t+1] + w(R_L))]]$$

$$s3 = [\beta(c) * (F[1, z(r-1), c-2, t+1] + w(R_H)) + (1-\beta(c)) * (F[1, r, c-2, t+1] + w(R_H))]]$$

Furthermore, $z(r-1) \in [0, 1]$ and

$$w(R) = \begin{cases} R & \text{if } r = 1 \\ 0 & \text{if } r = 0 \end{cases} \quad (5)$$

For reproductive pay-offs R_L and R_H (for low-intensity display in $s2$ and high-intensity display in $s3$, respectively), see Table 2.1.

I coded the model using R (R Core Development team 2010). The output is a multidimensional decision matrix in which I can “look-up” the optimal strategy for attractive and unattractive birds for each possible combination of states (body condition, lek attendance, territory status, and time in the season). I then simulate cohorts of males forward throughout the two seasons, assuming that each male follows the optimal behavior identified by the SDP model. The forward simulation allows me to compare the behavioral and condition trajectories of males starting with different body condition states.

The Forward Simulation

I simulated eight cohorts of $N = 100$ males with identical attractiveness and body condition states (see Table 2.2). I assume that at the beginning of the first season all males are off the lek, and half of the males own a territory and half do not. Males follow the optimal behavioral decision identified by the SDP model forward throughout time from $t = 1$ to $T = 60$, given that they survive each time step. Whether a male survives, gains reproductive success, and gains or loses a territory is based on his body condition, behavioral tactic followed (i.e., $s1$, $s2$, or $s3$), and the associated state-transition parameter probabilities from the SDP model. For example, on day 15 of the season, if a male is following $s2$ on the lek with a body condition state of 35 and no territory, the probability of surviving to the next time step is $\lambda(35) = 0.97$, gaining a territory is $\beta(35, 0, s2) = 0.15$, and gaining a reproductive payoff is $f(15) = 0.68$ (given that he gains at territory). I draw three random numbers (using the *runif* function in R)—if the first is less than or equal to 0.97, the male survives to the next time step. If the second random

number is less than or equal to 0.15, the male gains a territory. Finally, if the third random number is less than or equal to 0.68, the male gains a reproductive payoff if he owns a territory. I follow this method for all males in all time steps and recorded lek attendance, territory status, body condition, and behavior of males throughout the season in each of the eight cohorts. All surviving birds in each cohort behaved exactly the same throughout the season. Thus, I represent the forward simulation with the cohort average of each state variable.

In order to examine the population variance in body condition over time, I simulated a population of 100 males that varied in body condition at the beginning of the season. At the beginning of the season, assigned body condition states were drawn from a truncated normal distribution (Mean = 30, SD = 6, with body condition limited within the range of 18-42). The population consisted of half attractive and half unattractive males. Each half was further subdivided equally into males that owned a territory in the first time step and males that did not.

Changing Model Parameters

To explore how changes in the model parameters affect the behavior of males in the model, I explored the following parameter perturbations listed below. All other parameters and cohort simulations were kept identical to the baseline model.

1. *Female attendance functions f*: I examined scenarios with (a) “no reproductive synchrony” (Fig 2.3, solid line) with $f(t) = 0.6$ for all t and (b) “high reproductive

$$\text{synchrony” (Fig 2.3, dotted line) with } f(t) = \begin{cases} 0.1 + 0.045t & \text{if } 1 \leq t \leq 21 \\ 1 & \text{if } 21 \leq t \leq 25 \\ 1 - 0.1667(t - 25) & \text{if } 25 \leq t \leq 30 \end{cases}$$

2. *Between-season survival*: I increased between-season survival $\lambda_{=31}(c)$ to (a) 60% and (b) 80% of the daily survival function $\lambda_{t=30}(c)$.

3. *On-lek survival*: For some bird species, predation risk on the lek is likely to be higher than off the lek (Boyko et al. 2004). I explored two survival scenarios: (a) daily survival on the lek is 99.4% of the off-lek survival (a value estimated from Greater sage-grouse data, assuming that higher breeding season mortality is due to on-lek predation:

R.Gibson, unpublished data); (b) daily survival on the lek is 90% of the off-lek survival.

4. *Off-lek territory loss*: The probability of losing a territory when foraging off the lek following $s1$ increased to (a) $\alpha = 0.2$ and (b) $\alpha = 0.3$.

5. *Pay-offs associated with mating display of attractive and unattractive males*: Low intensity display ($s2$) of attractive males results in a lower expected fitness than high intensity display ($s3$) of unattractive males (expected fitness values are switched compared to the baseline model in Table 2.1, instead $R_L = 1$ for attractive male and $R_H = 5$ for an unattractive male).

6. *Handicap model versions*: In the baseline model attractive and unattractive males differ only in the reproductive pay-offs they receive during display. I also investigated two other scenarios based on the handicap model of sexual selection (Zahavi 1975; Grafen 1990; Getty 1998) in which attractive males and unattractive males differed in (a) only energy costs of display, or (b) both energy costs of display and reproductive pay-offs (see Table 2.3).

RESULTS

The Baseline Model

The SDP behavioral decision array was the same for males in all attractiveness, attendance, and territory states, and only varied with body condition c and time in the season t (Fig 2.4). Males in body condition states above 30 are predicted to always follow $s3$ (high-intensity display) on the lek. The range of states over which following $s2$ (low-intensity display) and $s1$ (foraging off the lek) is optimal declines throughout the seasons (Fig. 2.4). This is presumably because the future fitness of males declines as each season progresses.

In the forward simulations, initial body condition but not male attractiveness affected the weight loss trajectory, territory status, and survival of males during the first season (Fig 2.5A-C). Males that began with higher body condition states (30 and 40) both maintained a higher body condition throughout the first two-thirds of the season and started high-intensity display (indicated by the decline in body condition) earlier than males with initially lower body condition states (20 and 15) (Fig 2.5A). Because attractive and unattractive males gain different reproductive payoffs when following $s2$ and $s3$, seasonally accumulated reproductive pay-offs differed between attractive and unattractive males surviving to day 30. However the number of males surviving to day 30 did not differ between attractive and unattractive males (Fig 2.5D).

In the forward simulation of a population in which initial body condition at the start of the simulation was assigned following a normal distribution, both the mean and variance in male body condition decreased through the first season (Fig 2.6).

At the start of the second season in all forward simulations, surviving males retained their previous attractiveness level but were assigned a new randomly drawn initial body condition state independent of their condition at the start of the first season (see Methods). In the forward simulations all eight cohorts of males followed the same behavioral trajectory during the second season, ending with condition levels that were too low for most of the males to survive (details not shown). This prediction is due to the model assumption that future fitness must be zero at the end of the second season. Because this assumption is unrealistic in the context of lekking males in the wild (as in nature males do not know whether they will survive another season), I present forward simulation predictions only for the first season.

Changing Model Parameters

I also adjusted six different parameters used in the baseline model to determine how both the SDP predictions and forward simulation results for the first season changed in comparison to the baseline model. I refer to males starting the breeding season with a body condition of X as X body state condition males.

1. *Female attendance functions f* : Changing the female attendance function from “moderate reproductive synchrony” to “no reproductive synchrony” caused decreased foraging ($s1$) early in the season. The 20 and 15 body condition state males maintained body condition at 20 throughout the season, which is at a slightly lower condition level than in the baseline model. These males engaged in high-intensity display ($s3$) only during the last three days of the season, 5 days after the 30 and 40 body condition males

began high-intensity display (Fig 2.7A). When the female attendance function was changed to “high reproductive synchrony,” males in lower body condition states (15 and 20) foraged for the first third of the season, and maintained a body condition in the upper 20s before the late-season decline due to high-intensity display (Fig 2.7C). In both scenarios, the relationship between initial condition and both seasonally accumulated reproductive success and survival remained the same as in the baseline model (Fig 2.7B &D).

2. *Between-season survival*: Increasing the between-season survival rate from 40% to 60% and 80% of the daily survival rate had little effect on the SDP and forward simulation. Compared to the baseline model, males with lower body condition states (20 and 15) forage for one additional day off the lek at the beginning of the season, and all males delay high intensity display s_3 , and hence consequent of body condition decline, by one day.

3. *On-lek survival*: Decreasing on-lek survival slightly to 99.4% of the off-lek survival resulted in increased foraging (following s_1) for the first eight days of the season for males with body condition states lower than 30 and therefore an increase in maintained body condition throughout the season compared to the baseline model. In addition, males in higher body condition states began high-intensity display (s_3) four days earlier than in the baseline model (Fig 2.8A). The relationship between initial body condition and both seasonally accumulated reproductive success and survival remained similar as in the baseline model (Fig 2.8B). However, in the second scenario tested with high on-lek

predation (0.9), males no longer used low-intensity display (s_2) as a strategy. Males in all body condition states increased or decreased body condition to 30 (or maintained body condition at 30), and then alternated back and forth between foraging and high-intensity display (Fig 2.8C). Like the baseline model, attractive males had higher seasonally accumulated reproductive success than unattractive males. Most interesting is that males in lower body condition states (15 and 20) had increased survival compared to the baseline model because they were off the lek in the first part of the season (Fig 2.8D). This is in comparison to males with higher body condition states (30 and 40) that attended the entire season and therefore had lowered survival but higher reproductive success (Fig 2.8D). In addition, males in lower body condition states that foraged off-lek were less likely to have a territory in comparison to the baseline model as they consistently were off the lek, but as soon as they started alternating between foraging and high-intensity display, they were almost as likely to have a territory as males in initially higher body condition (Fig 2.9).

4. *Off-lek territory loss*: Increasing α (the probability of losing a territory if foraging off-lek following s_1) to higher values did not affect the results of the model. This suggests that the necessity of territory ownership to gain reproductive success does not affect lekking behavior under the modeled scenarios.

5. *Pay-offs associated with mating display of attractive and unattractive males*:

Switching the payoffs between attractive males following s_2 and unattractive males following s_3 gives qualitatively the same SDP and forward simulation results as the high

on-lek predation case in 3 above (Figs 2.8C & D, 2.9). Males alternate back and forth between foraging off-lek ($s1$) and high-intensity display ($s2$) on the lek, because the payoff of low-intensity display ($s2$) is so low (relative to high-intensity display) that it never pays to engage in low-intensity display. Unattractive males were able to gain about half of the seasonally accumulated reproductive success of attractive males (Fig 2.10).

However, the relationship between body condition and survival was in concordance with the baseline model (Fig 2.10), and survival did not decline with increasing initial condition as under the high-predation case (Fig 2.8D).

6. *Handicap model versions*: In both handicap model scenarios, attractive males have the same condition trajectory as the baseline model (Fig 2.11B). Unattractive males have almost the same condition trajectory as in the baseline model, but delay high-intensity display ($s3$) by two days (Fig 2.11 A&B). These trajectories are the same for the scenario (a) with differential costs only, and scenario (b) with both differential costs and differential reproductive payoffs. Reproductive success differs between the two scenarios. In the first scenario with unequal costs only, “unattractive” males with higher costs reach seasonally accumulated reproductive payoffs that are almost as high as those of “attractive” males with lower costs. In the second scenario with unequal reproductive payoffs as well as costs, the relationship between body condition and seasonally accumulated reproductive payoffs of both attractive and unattractive males is very similar to the baseline model (Fig 2.11 C& D). Similarly, the relationship between body condition and survival was comparable to the baseline model for both scenarios (Fig 2.11C & D).

DISCUSSION

In my model, initial body condition largely determines the optimal behavioral trajectory males follow throughout the breeding season. Males with low body condition at the start of the season attend the lek rather than forage off the lek to increase body condition and therefore maintain a poorer body condition during the middle of the season. In addition, poor condition males delay the onset of high-intensity display thereby postponing a body condition decline relative to better-condition males. Males also maintain body condition in the range that provides the highest survival for the majority of the breeding season.

Other SDP models also predict that energy reserves play an important role in determining optimal male reproductive tactics. For example, Lucas & Howard (1995) found that male frogs with low energy stores should forage to participate in choruses later on in the season. Similarly, other models of frog chorus dynamics predict that males with low energy reserves should resort to the less energetically costly option of being satellites to other calling males (McCauley et al. 2000; Lucas et al. 1996). In a model examining ungulate male lek behavior, Isvaran & St. Mary (2003) found that males with higher energy states chose the more energetically expensive but higher reproductive payoff strategies compared to males with lower energy states throughout the breeding season, which led to increased reproductive success. Hence, all of these models predict that initial body condition affects the optimal reproductive tactic. It has been previously suggested that all models investigating alternative mating tactics should incorporate frequency dependence by using a game theoretic framework (Lucas et al. 1996; Lucas & Howard 2008). However, non-game theoretic models, such as mine and Isvaran & St, Mary

(2003), give similar predictions about how energy reserves affect reproductive behavior at the individual level.

I found that the cost of display (condition loss) affects the behavior of males in the model versions incorporating differential costs of display. With an increase in the cost of high-intensity display, males delay both entry onto the lek and the onset of maximum effort by a day. Males with higher display costs do not attend the lek for as long or perform high-intensity display for as many days as males with a lower cost of display. As a consequence, males with a higher cost of display receive lower cumulative reproductive pay-offs by the end of the season. The effect of changing display costs is independent of attractiveness. Lucas et al. (1996) also found that an increased energetic cost of calling reduces calling duration in frog choruses in a SDP model.

The relative reproductive pay-offs between alternative display behaviors also affect the optimal behavioral strategy over the course of the season. When the reproductive pay-off of males engaging in low-intensity display was decreased from one-half to one-tenth of the payoff of males in high-intensity display, males no longer used low-intensity display. This is presumably because the reproductive payoffs of low-intensity display were too low relative to high-intensity display and it was always better to use high-intensity display on the lek even at the cost of reduced body condition.

In addition, males with lower body condition changed their optimal behavioral strategy and matched lek attendance with female attendance to maximize mating opportunities. Altering the female attendance function to be more or less synchronous caused only low-condition males to change their behavior. Under high female reproductive synchrony, low-condition males foraged off the lek for the first third of the

season. With no female reproductive synchrony, low-condition males always attended the lek. Lucas & Howard (1995) also found that males synchronize chorus attendance with female arrival rates in their frog chorus model.

Lek behavior can also be altered by changes in predation risk. From my model and from Boyko et al. (2004), we know that predation risk can decrease the lek attendance of males during the breeding season in SDP models. In one version of my model, I included higher on-lek mortality compared to off-lek mortality in order to mimic the effects of higher on-lek predation. Even a slight decrease in survival on the lek caused a decrease in early season lek attendance for low-condition males and caused all males to start high-intensity display earlier in the season. Under higher levels of on-lek mortality, a strong reproductive-success survival trade-off became apparent. Males in lower body condition states showed increased survival relative to those in higher body condition states because low-condition males did not attend the lek for the first portion of the season and therefore did not face increased predation risk. In contrast, in the model scenarios without a difference between on- and off-lek mortality, all males consistently attended the lek after day 7 and males with an initial body condition of 30 showed the highest survival (followed in order by males with initial body conditions of 20, 15, and 40).

My model predicts that males lose mass over the course of the breeding season, which is supported by many studies in polygynous species (see Introduction). However, no empirical studies that I know of demonstrate the decline in the variance in body condition of adult males through the breeding season predicted by my model (Fig 6). Because males did not survive beyond two seasons and fully recovered body condition

between seasons, males had very similar future reproductive success at the start of the second season. This led to a convergence of body condition at the end of the first season. In nature, expected future reproductive success likely varies widely between individuals, potentially leading to different optimal mating strategies and hence different body condition trajectories through the breeding season.

Empirical support also exists for the idea that energy reserve levels at the beginning of the season affect both behavior and mass loss during the breeding season. One example is yearling and adult males in both Greater and Gunnison sage-grouse. In both species, adult males are heavier than yearlings at the start of the breeding season. In Greater sage-grouse, adult males from a Colorado population lost about two times as much mass as yearlings over the course of the breeding season (Beck & Braun 1978). In an Eastern California population, adult males lost mass whereas yearlings gained mass during the breeding season (R. Gibson, unpublished data). In Gunnison sage-grouse, adult males also tended to lose weight while yearlings gained weight during the breeding season (J.R. Stiver, unpublished data). Mass loss by adult sage-grouse males likely reflects increased time spent on the lek (Wiley 1973). These sage-grouse studies suggest that males with high body condition (adults) are attending the lek and subsequently losing mass from lekking activity, whereas males in poorer body condition (yearlings) are gaining mass presumably due to increased foraging. This is in concordance with the model predictions in that males with higher body condition are more likely to attend and expend energy on the lek.

Time invested into breeding may also differ between individuals that have differing levels of energy reserves in other non-lekking species. Male mountain goats that

are older tend to be heavier and also spend more time in rutting behaviors than younger males (Mainguy & Côté 2008). Similarly, younger male red deer are lighter and have a delayed start to the rutting season (Gibson & Guinness 1980), just as my SDP model predicts that males with less energy reserves at the start of the breeding season delay the onset of lekking. Although age may be a confounding variable, all of these studies suggest that the behavior of males is affected by body condition at the start of the breeding season.

Interestingly, empirical support exists for one of the specific predictions in the on-lek predation scenarios. Under high levels of predation risk on the lek, the model predicts an inverse relationship between reproductive success and survival. Males with high initial body condition showed the lowest survival but also the highest reproductive success because they attended the lek and faced increased predation but also obtained reproductive success from matings. This trade-off is found in Gunnison sage grouse, in which the lighter yearling males that attend leks less frequently have lower reproductive success but higher survival than adult males (JR Stiver, unpublished data).

Overall, I found that initial body condition was the most important factor determining lek attendance and lek activity in my models. Males with initially lower body condition were predicted to forage early in the season and delay the onset of maximum display effort compared to males with initially higher body condition. As a consequence, these males also maintained a lower body condition throughout the season. Empirical evidence also supports the model prediction that increased male body condition at the beginning of the breeding season increases time spent in reproductive

activities. This phenomenon could be further explored by empirical studies that investigate the causes and consequences of variation in individual body condition.

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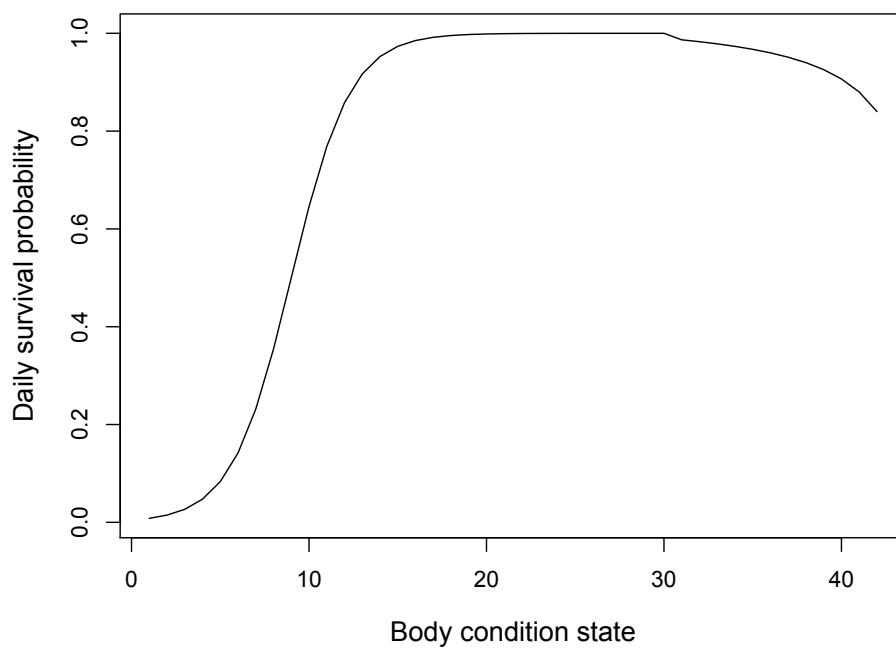


Figure 2.1: The modeled relationship between daily survival and body condition state. Males above 30 are penalized for being overweight, and males below 19 are penalized for being underweight.

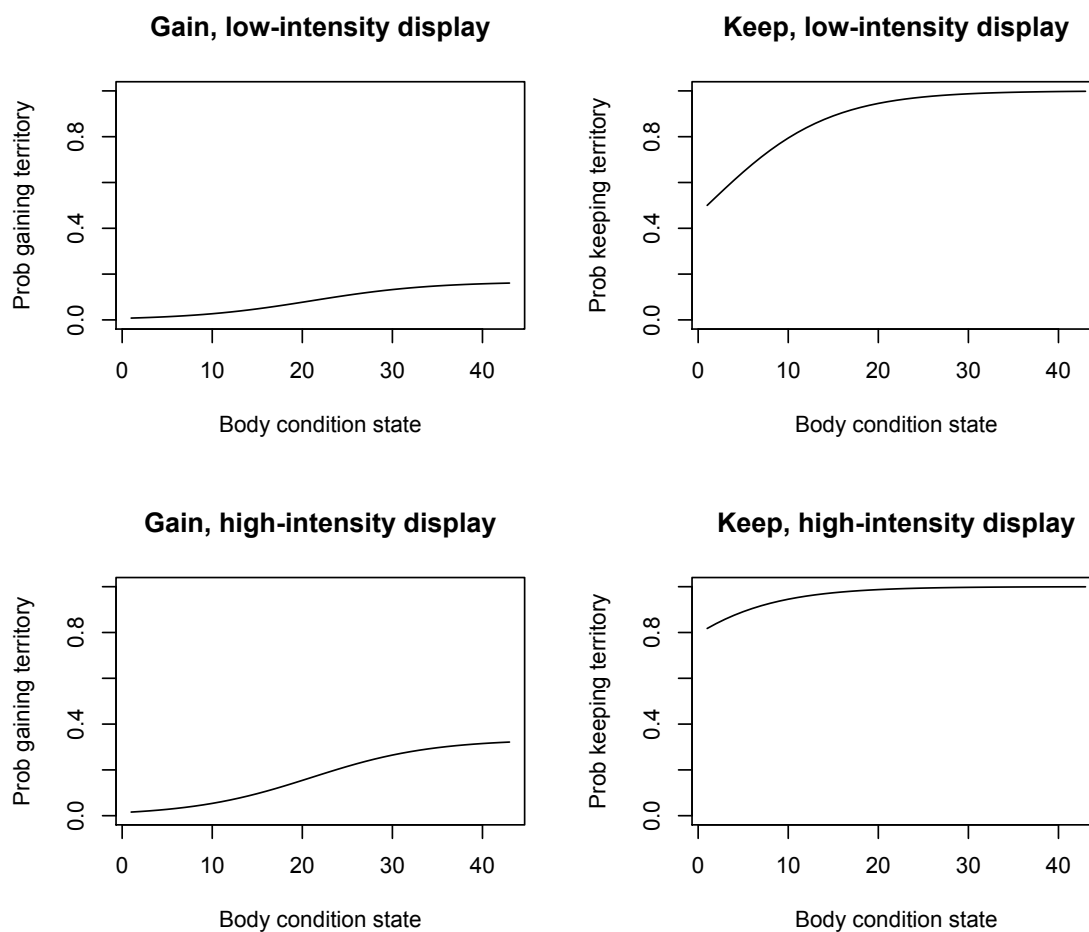


Figure 2.2: The probability of gaining and keeping a territory in each time step in relation to body condition (x-axis) and strategy (low-intensity display: upper panels, high-intensity display: lower panels) for lek-attending males.

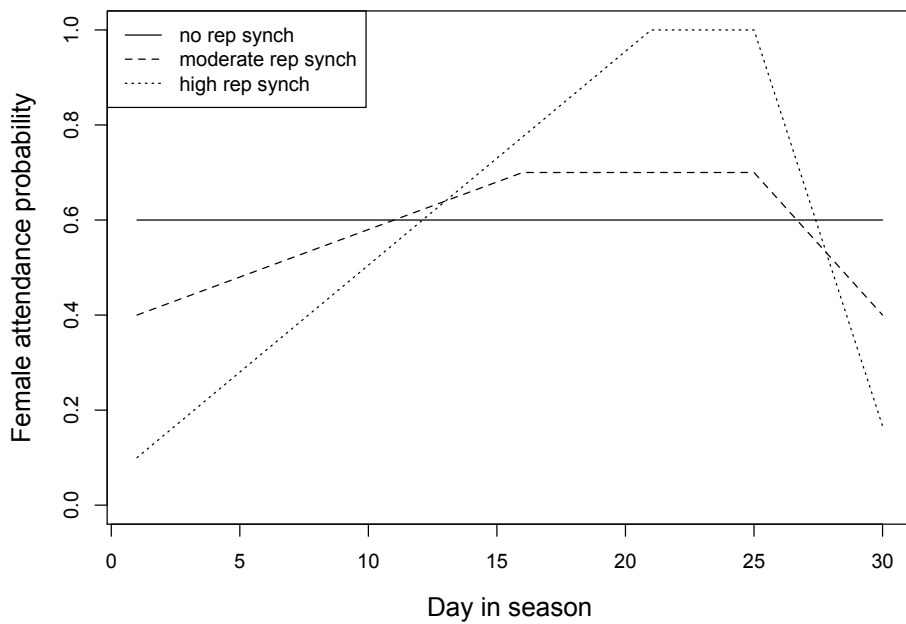


Figure 2.3: The three female attendance reproductive curves that differ in degree of synchrony. The moderate reproductive synchrony curve is used in the baseline model. All three curves have the same integral area.

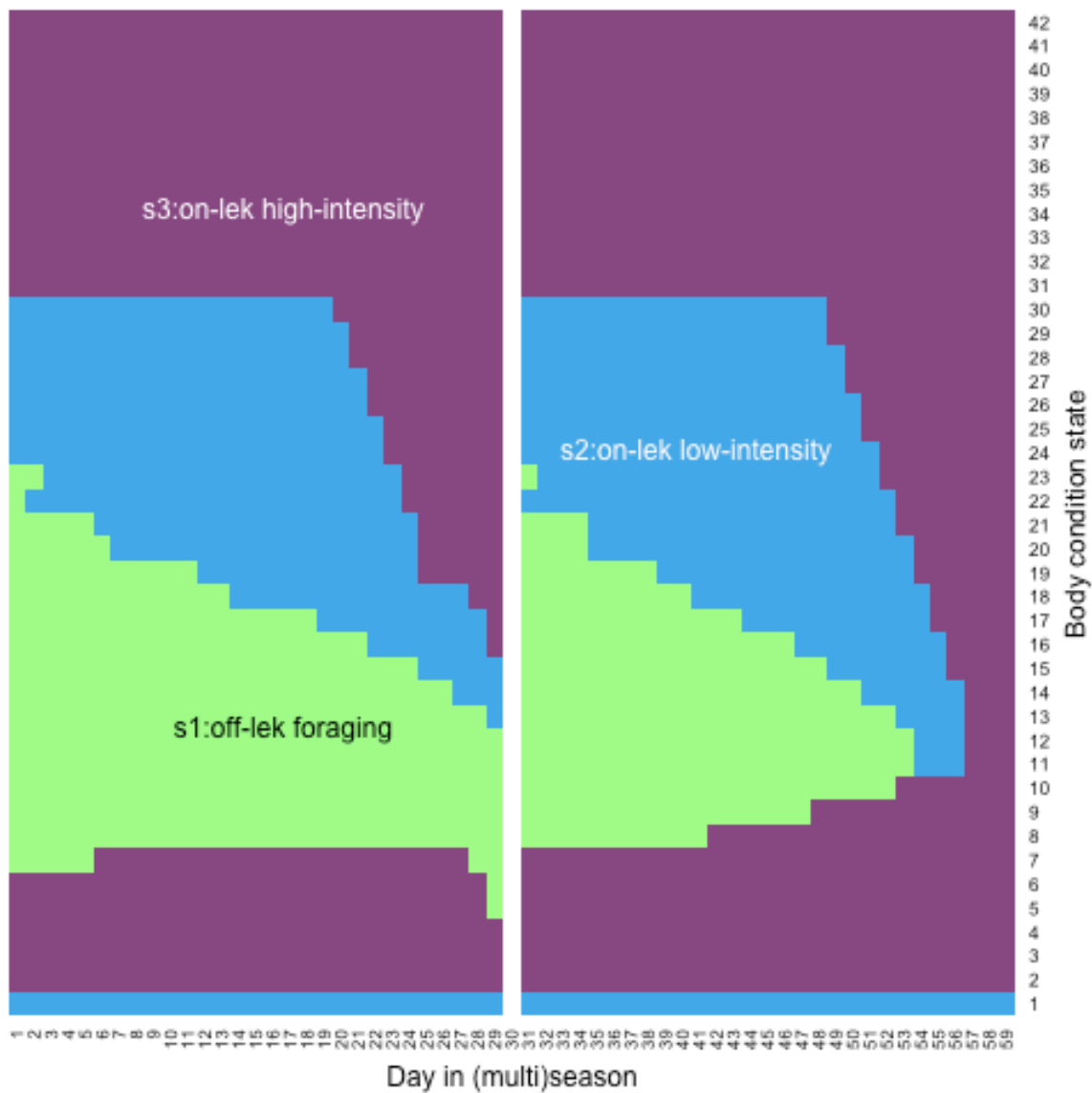


Figure 2.4: The SDP optimal decision matrix for the two 30-day season baseline model. Different colors denote the three different strategies males should follow based on body condition c and time t in the season. The same decision trajectory was produced for males in all possible combinations of attractiveness level, territory state, and lek attendance state.

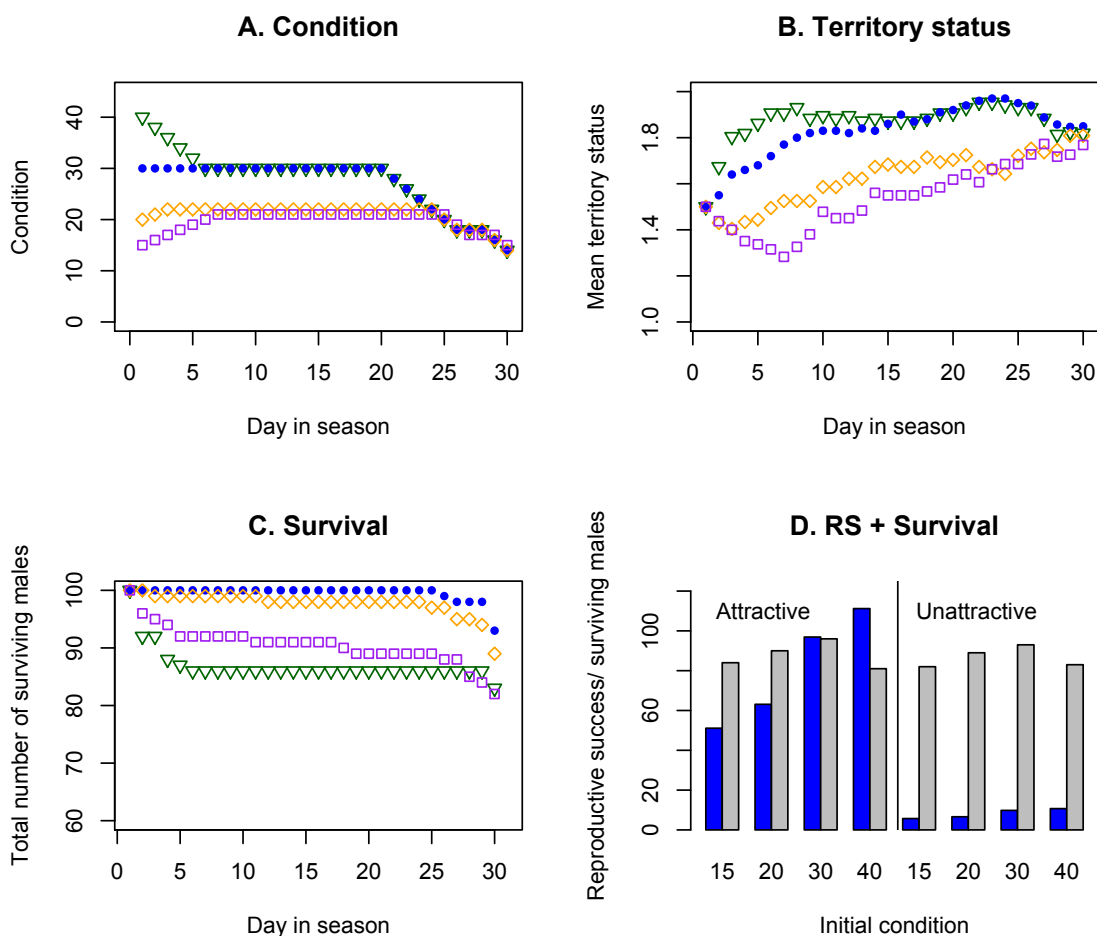


Figure 2.5: Baseline forward simulation condition trajectory (A), mean territory status (B), survival curve (C), and end of season reproductive success and number of surviving males (D) for the first season. All parameters were equivalent between attractive and unattractive males except for reproductive success (D). In panels A-C, green triangles, blue circles, yellow diamonds, and purple squares represent the cohorts of males with initial body condition states of 40, 30, 20, and 15, respectively. In panel D, blue bars represent the reproductive success and grey bars indicate the number of surviving males at the end of the first season.

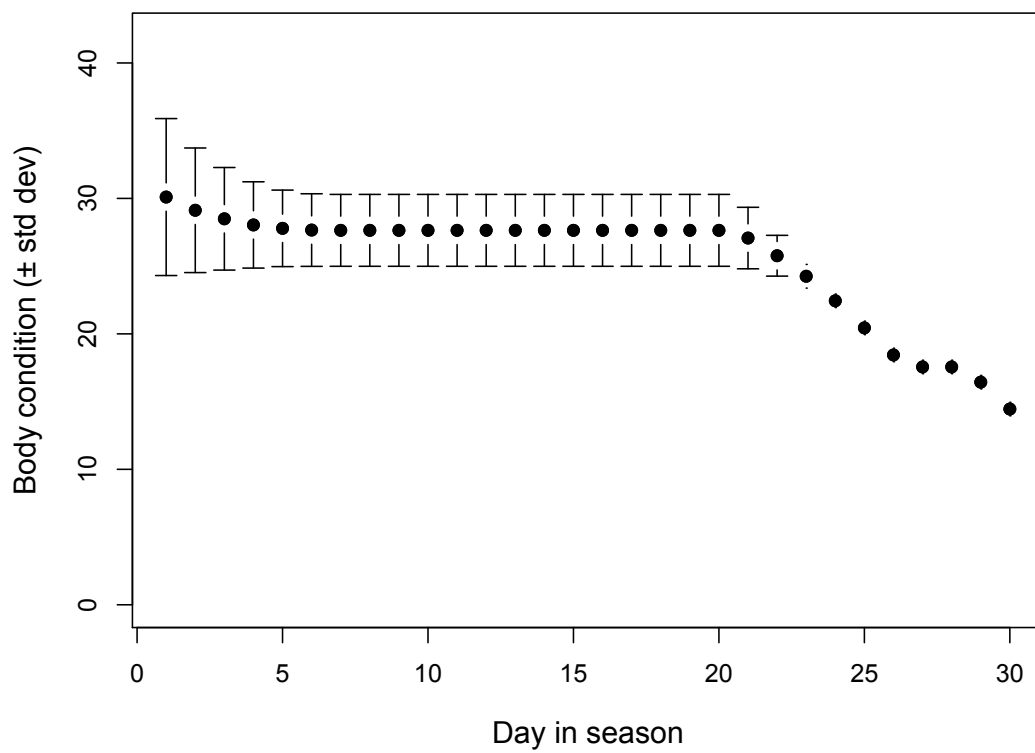


Figure 2.6: Body condition means and standard deviations through time for a population simulation of 100 males. These males were initially assigned body condition states following a normal distribution (Mean=30, SD=6).

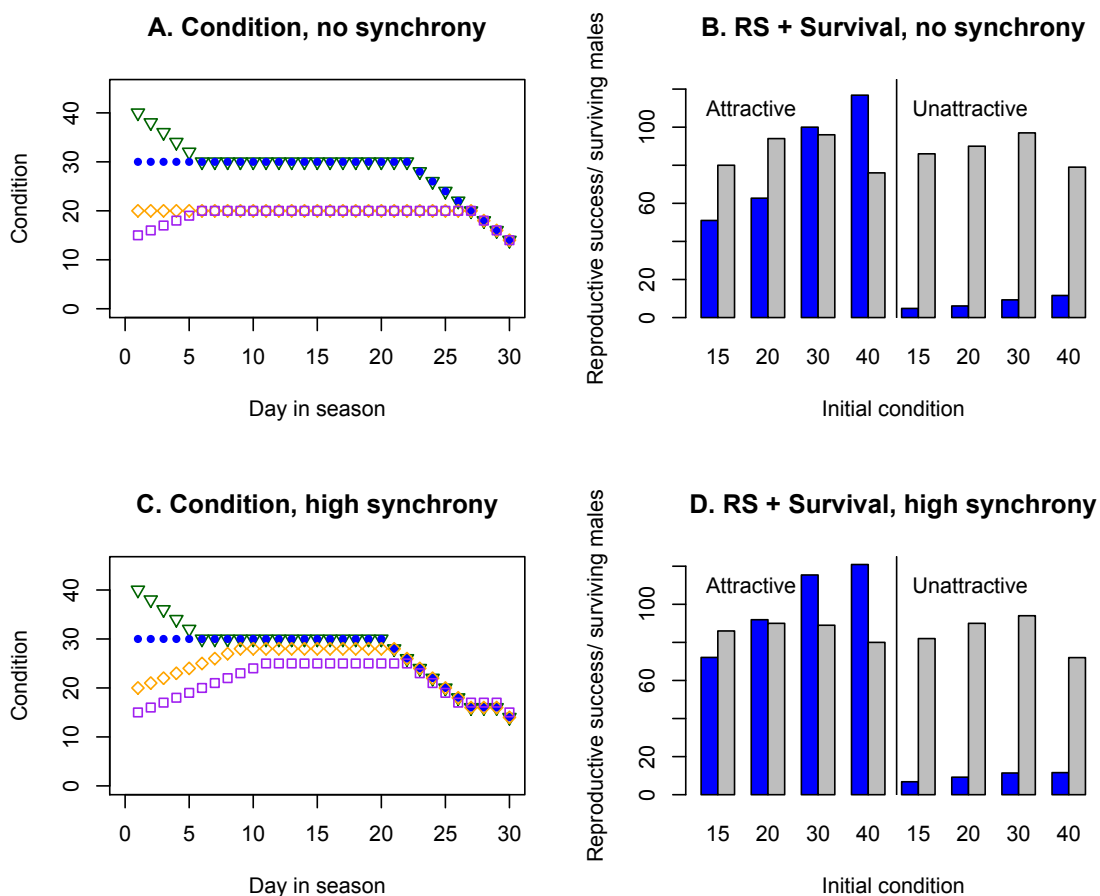


Figure 2.7: Male body condition trajectories, reproductive success, and the number of males surviving to day 30 under no reproductive synchrony and high reproductive synchrony female attendance curves for the first season. See Figure 5 legend for explanation of symbols.

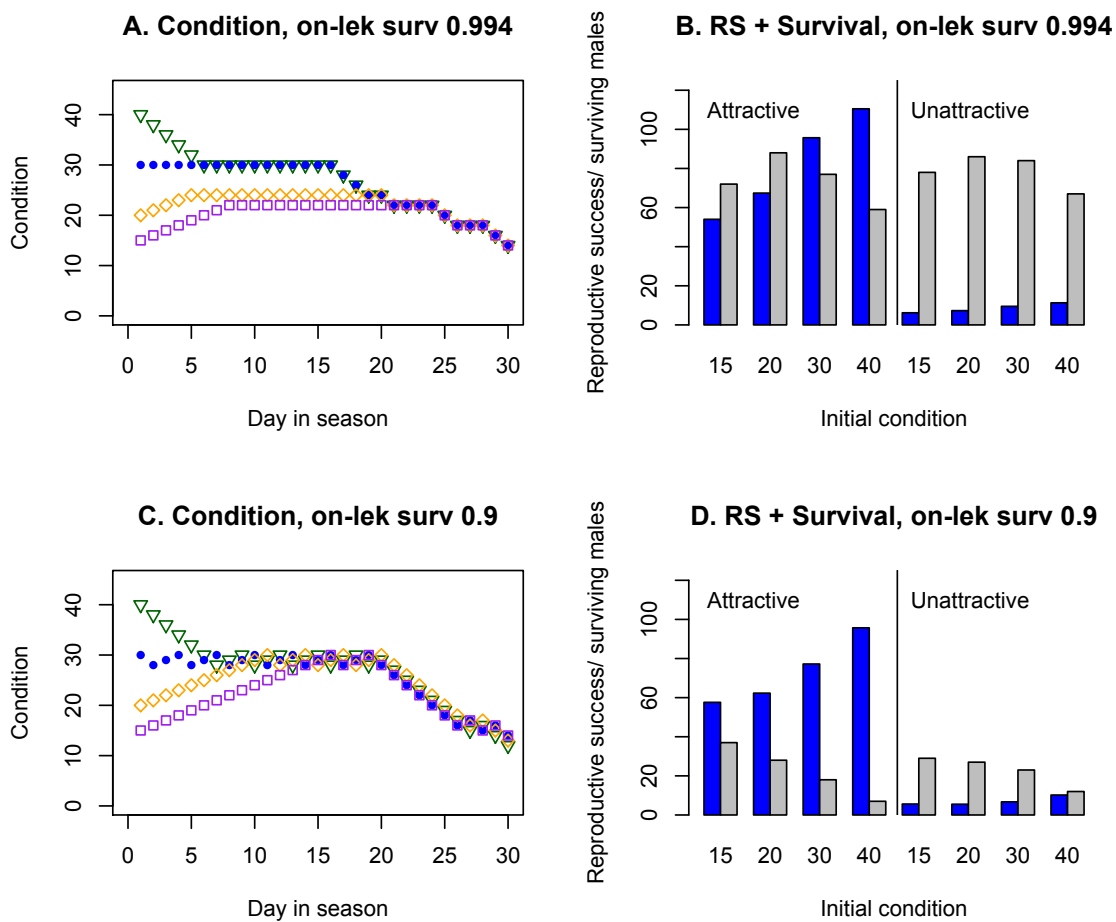


Figure 2.8: Male body condition trajectories, reproductive success, and the number of males surviving to day 30 for the first season under slight and high on-lek predation (0.994 and 0.9, respectively of off-lek survival). See Figure 5 legend for explanation of symbols.

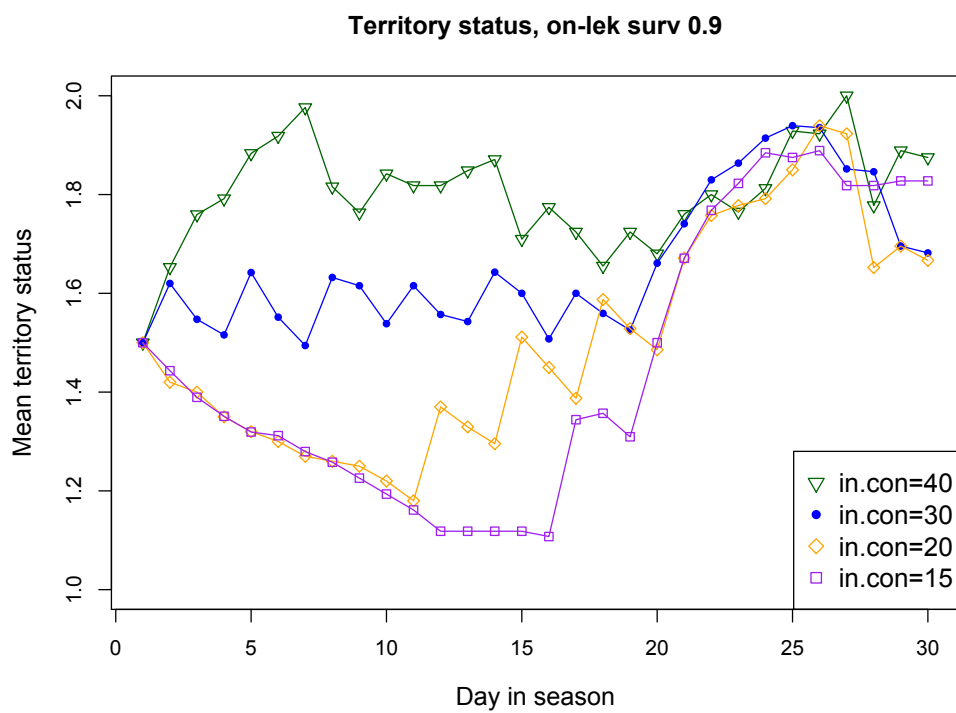


Figure 2.9: The average territory status of males under the high on-lek predation scenario (0.9 of off-lek survival).

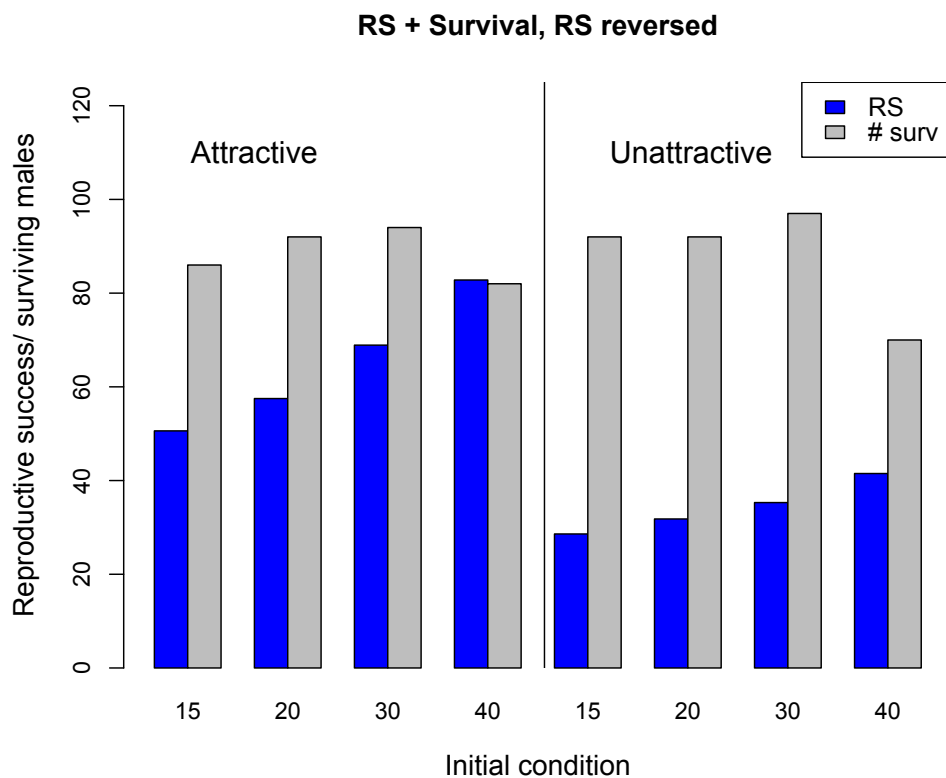


Figure 2.10: The reproductive success and number of surviving males when the payoff of low-intensity display is reduced from 1/2 to 1/10 the payoff of high-intensity display for both attractive and unattractive males.

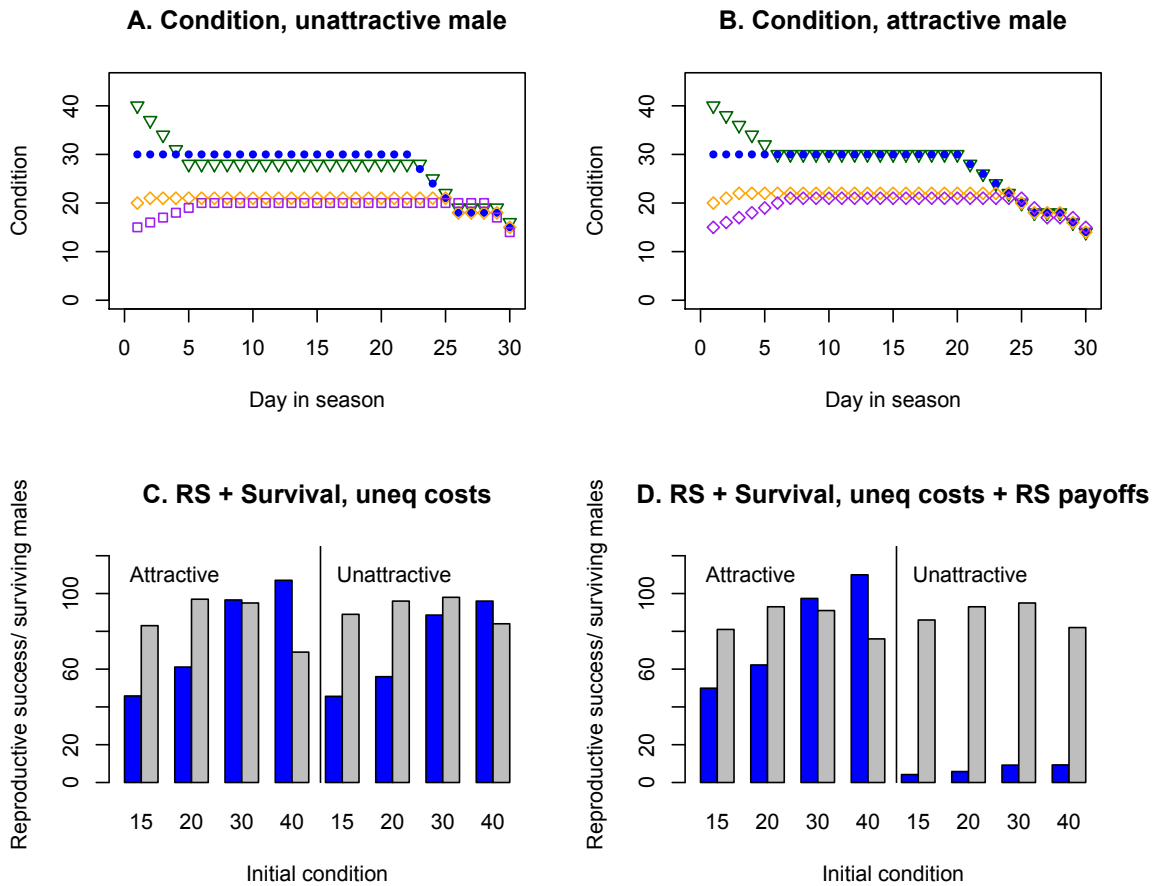


Figure 2.11: Male body condition trajectories, reproductive success, and the number of males surviving to day 30 under the handicap scenarios. The upper panel shows condition trajectories for unattractive (A) and attractive males (B). In both cases the trajectories were the same for scenarios with unequal costs only versus both unequal costs and reproductive payoffs. The lower panel shows reproductive success and survival in the scenarios with unequal costs (C) and with both unequal costs and reproductive payoffs (D). See Figure 5 legend for explanation of symbols.

Table 1. The reproductive payoffs R , change in body condition Δc , and equation (2) parameter values (a , b) for gaining or keeping territories for each behavior choice d . R_L is the reproductive payoff for low-intensity display and R_H for high-intensity display. $r = 0$ means the male has no territory, $r = 1$ means the male owns a territory.

Parameter		behavior, d		
		$s1$ (foraging)	$s2$ (low-intensity display)	$s3$ (high-intensity display)
Reproductive Payoffs R		0	$R_L = 5$ for attractive male $R_L = 0.5$ for unattractive male	$R_H = 10$ for attractive male $R_H = 1$ for unattractive male
Δc		+1	0	-2
a	$r = 0$		6	3
	$r = 1$		1	1
b	$r = 0$		-20	-20
	$r = 1$		0	10

Table 2. Assigned initial states for the eight cohorts in each forward simulation. Each cohort consisted of 100 males of which 50 owned a territory and 50 did not. “A” refers to attractive and “U” to unattractive males.

Cohort	Body condition at $t = 1$	Level of attractiveness
1	15	A
2	20	A
3	30	A
4	40	A
5	15	U
6	20	U
7	30	U
8	40	U

Table 3. The costs and reproductive payoffs for high- and low-intensity display in the two modeled handicap scenarios: (a) differential costs only, and (b) both differential costs and differential reproductive payoffs.

(a)	$s2$ (low-intensity display)		$s3$ (high-intensity display)	
	Attractive	Unattractive	Attractive	Unattractive
Reproductive Payoff	5	5	10	10
Δc	0	0	-2	-3
(b)	$s2$ (low-intensity display)		$s3$ (high-intensity display)	
	Attractive	Unattractive	Attractive	Unattractive
Reproductive Payoff	5	0.5	10	1
Δc	0	0	-2	-3