DETERMINANTS OF PATERNAL CARE IN RED-WINGED BLACKBIRDS

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Abstract

Red-winged blackbirds are polygynous songbirds that exhibit facultative paternal care, with males helping at a fraction of nests in their harem. Understanding facultative paternal care is key to understanding the evolution of biparental care. Here I examine paternal care in red-winged blackbirds in relation to a male's opportunity to attract additional mates, and the value of the brood to be fed. I used data I collected in 2009 in conjunction with a video library of red-winged blackbirds nesting (n = 221 nests) in southern Manitoba over 17 consecutive years. More than half the nests received paternal care by day 8 of the nestling period. Paternal care was associated most strongly with brood size, brood age, brood structure and habitat type. Older and larger broods were fed more often. Broods in marshes were fed less often than broods in ditches. The high rate of paternal care exhibited in this population compared to more southern and coastal populations appears to be due to the short nesting season and limited opportunities for breeding males to attract additional mates.

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Introduction

Most birds and mammals provide extensive care for their offspring. In species which exhibit biparental care, sexual conflicts can arise as to how much care each parent should allocate to a given brood (Akçay and Roughgarden 2009). In such species, offspring benefit from the care they are given, but each parent suffers a reduction in future reproductive potential related to the amount of effort they expend on their current offspring (Houston *et al.* 2005). A fundamental life history question for all species asks: who should care for the offspring, and how much should they care (Clutton-Brock, 1991)?

The extent of parental care varies widely across the animal kingdom, from some species offering little to no care, to others who invest years of their lives to ensure the survival of their offspring. As new species evolved and diverged from one another, new behaviours related to caring for offspring began to develop as well. In marine invertebrates, a very low level of parental care coupled with high numbers of gametes became the norm. By releasing large numbers of gametes into the ocean currents, marine invertebrates play a sort of lottery that guarantees a few surviving offspring with a minimum amount of post zygotic parental investment. On the other end of the spectrum is the group of long lived vertebrates (including humans) that carry out obligate biparental care for years in

an attempt to raise a very small number of offspring. Many other parenting strategies have evolved including uniparental (monoparental) maternal care (common in most mammals), uniparental paternal care (common in some fish and bird species), and facultative biparental care (Clutton-Brock, 1991), which will be the topic of this thesis.

Biparental care (both facultative and obligate) makes up 81% of all care in wild birds (Cockburn 2006). This is likely due to the fact that birds must contend with a number of potential problems while rearing their offspring. The first problem is that eggs must be simultaneously incubated and defended. Once the eggs hatch, brooding and feeding are mutually incompatible activities. Under uniparental care, the parent must leave the nest to forage, but this leaves the nestlings un-warmed and vulnerable to predators. Dividing the tasks between two parents, with one parent feeding while the other parent protects and warms the nestlings is an obvious evolutionary solution. This problem with incompatible activities (as described above) is more closely associated with altricial birds (e.g., most songbirds and other species with relatively immature offspring at birth) than with their precocial (e.g., ducks and other species born relatively independent of their parents) counterparts. Altricial nestlings are

defenceless as they start their lives and their nests are often easily found by predators (Clutton-Brock 1991).

Facultative biparental care is a parental care strategy in which one parent (usually the female) must care for the offspring to ensure their survival, while the other parent (usually the male) is given a choice of behavioural trade-offs. The most common is the choice between raising the current brood and advertising for more mates (Patterson *et al*. 1980). Sexual conflicts ensue since both parents wish to expend the least amount of energy they can, while also ensuring the survival of their offspring. Parental care theory deals with questions of how parents decide upon who raises offspring and how much care each parent allocates (Akçay and Roughgarden 2009).

Most research into the area of parental communication within biparental care species has centered on compensation. Theory states that for biparental care to exist, when one parent reduces their parental allocation, the other should never increase their care enough to make up for what was lost; the term for this behaviour is partial compensation (Houston *et al.* 2005). Two different models for parental communication in biparental species have emerged in recent years. The sealed bid model states that each parent has a predetermined level of parental care that they are willing to expend, and they will not react to a

reduction in their mate's contributions (Schwagmeyer *et al.* 2002). The negotiation model (Houston and McNamara 1999, cited in Suzuki and Nagano 2009) allows for some communication between parents. One can react to a reduction in the other's efforts, but should never completely compensate for what was lost (since this could lead to exploitation of the compensating parent by the parent that reduces its personal efforts). Depending upon the study species, the experimental set-up, and the geographical location of the population, compensation levels have been found to vary greatly. Although numerous bird species have been found to compensate for the removal or handicapping of their partner by provisioning at a higher rate (Houston *et al.* 2005, Hind and Kilner 2007), little to no compensation was seen when the house sparrow (a model for the monogamous biparental care system) was examined closely (Schwagmeyer *et al.* 2002). The question of compensation was even examined using the monogamous burying beetle *Nicrophorus vespilloides.* In this species, males reacted to the removal of the female, but the opposite was not found to true (Suzuki and Nagano 2009).

Red-winged blackbirds (*Agelaius phoeniceus*) are polygynous songbirds that exhibit facultative biparental care (Beletsky 1996, Searcy and Yasukawa 1995, Westneat et al. 1995). Male redwings hold vigil over a harem of females (average

2-6) for the entire breeding season (Beletsky 1996). The facultative biparental care that this altricial species exhibits is asymmetrical with the female acting as the obligate caregiver. She builds the nest, invests resources in egg laying, incubates the eggs, and provides most of the food for her nestlings (Beletsky 1996, Searcy and Yasukawa 1995). Patterson (1991) described research from the 1960's and 1970's reporting that males were not caregivers, but almost exclusively defenders of their personal territory (against predators seeking eggs and nestlings, and other male redwings seeking extrapair copulations). Starting in the 1980's researchers began to look more closely at paternal care of the nestlings, and found that in a number of populations males did indeed contribute to feeding nestlings (Patterson 1991).

Subsequent research has documented a number of variables that are associated with male feeding of the brood instead of advertising for new mates. Yasukawa *et al.* (1990) correlated increased male provisioning to brood size and nestling age. Muldal *et al.* (1986) correlated male feeding with the mass of the entire brood and noted a positive relationship. Whittingham (1989) found that males would feed nestlings in larger or older broods. She noted that males would only assist a female if the brood was more than three days old and contained at least three offspring. She also found that males frequently helped

feed nestlings in a brood where the female alone was unable to satiate the entire brood. Patterson (1991) found that males started feeding some broods on day four, and that they frequently fed larger broods when given a choice. Westneat (1995) also found that males fed older nestlings more frequently.

Here I examine paternal care in red-winged blackbirds in relation to two sets of factors: a male's opportunities to attract extra mates; and the potential value of the current brood. A male's ability to attract additional mates will depend upon when (greater potential early in the breeding season) and where (habitat type can influence harem size and potentially the male's confidence in paternity) he breeds. The value of the brood is likely governed by the number (nests containing more chicks being more valuable) and age (nests containing older chicks being more valuable) of nestlings. One brood characteristic that has yet to be examined in terms of paternal care is the presence and number of core and marginal nestlings. The value of the brood is expected to be higher in nests with more core nestlings.

Red-winged blackbirds and numerous other avian species are able to control the order in which their eggs hatch. If a female begins incubating some eggs before she finishes laying her full clutch, the eggs that received the extra incubation time will hatch first. Due to this hatching asynchrony, the core brood

(first group to hatch) is at a distinct advantage when compared to the subsequently hatching marginal brood. Depending upon the severity of the asynchrony, the marginal nestlings may be up to 2 days behind their core siblings in terms of food intake and growth, and under less than perfect conditions, they often perish (Forbes *et al.* 1997). Forbes (2005) explained that the core brood is representative of the number of offspring parents can expect to rear under normal ecological conditions. In this case, if conditions are average (in terms of food availability, weather, etc.) the marginal offspring will starve, but if conditions turn out to be above average the marginal offspring can be reasonably successful, and will likely fledge. By hatching nestlings asynchronously the female gives herself a number of expendable progeny that have potential to survive under optimal conditions.

The value of the brood may be affected by the presence or absence of a brood parasite such as a brown-headed cowbird (*Molothrus ater*). The brown-headed cowbird is an obligate brood parasite to more than 100 avian species (Kilner *et al.* 2004). Unlike other brood parasites (e.g., some cuckoos and honeyguides) the cowbird chicks do not directly attack, evict (except on rare occasions), or kill their nestmates (the host nestlings) (Kilner 2003, Rivers *et al.* 2009). Recent studies have found that cowbird nestlings have a higher success

rate when raised with one or two nestmates. By allowing host siblings to live, the cowbird gains access to a larger number of feeding events since feeding frequency has been correlated to brood size in many avian species. Cowbird nestlings that are raised alone, or with nestmates that are larger than them tend to fair poorly (Kilner *et al.* 2004).

The effects of habitat type on yellow-headed blackbirds (*Xanthocephalus xanthocephalus*), a species closely related to redwings (sharing nesting behaviours, mating systems, territories, and a place in the family Icteridae), was examined by Orians and Wittenberger (1991) and it was found that a number of habitat characteristics dictated harem size and the females' choice of nest location. Prey density was among the most important factors when it came time for a female to choose a male and a territory. Males on marshes with higher prey densities held larger harems. In terms of vegetation levels and territory size it was found that females preferred moderately sized marshes with medium cattail coverage and extensive channeling. Marshes that have higher vegetation levels or that are too narrow, allow for easy access to nestlings by terrestrial predators. Habitats with lower vegetation levels have few cattail supports, which are required for nest-building. Males that held these less than adequate territories had small or non-

existent harems. Small harems produce small numbers of offspring and increase the value of the brood.

In subsequent years, population density in red-winged blackbirds from differing habitat types was thoroughly examined by Vierling (1999). She found that harem size for redwings was stable between different habitat types (wetlands with or without the yellow-headed blackbird acting as a territorial competitor, in hayfields, in road and rail ditches, and in tallgrass prairies). Although the average harem size varied little across these habitats, the number of male redwings per hectare and the average number of fledglings per nest appeared to be quite dependent on habitat type. In natural habitats, males were recorded at much higher densities than in human-disturbed habitats; the ditch habitats had the lowest density of males, and the lowest fledgling numbers of any habitats she examined.

Previous studies have found varying levels of paternal care in red-winged blackbirds, from almost none in populations studied in Washington by Holm (1973) and Iowa by Blakely (1976) to frequent feedings in populations in New York (Yasukawa and Searcy 1982), Michigan (Fiala 1981), and Indiana (Patterson 1979) (all studies cited in Muldal *et al.* 1986). Some of the earlier studies had

small sample sizes, which could reduce the reliability of results. It is also likely that geographic variation plays a role in determining paternal care levels.

In more southerly and/or coastal regions, the breeding season is considerably longer. Due to this long breeding season, males are predicted to allocate less care to their existing broods for a number of reasons; the long breeding season deemphasizes the importance of any one brood's survival because it gives males many more opportunities to attract new mates. A warm and lengthy breeding season also makes it likely that prey items (insects and aquatic larva) will be more abundant, making it easier for a single female to provide enough for her brood (Beletsky 1996) . In some areas with long breeding seasons, double broods, which occur when a female raises a first brood to fledging age before laying another batch of eggs, have even been reported (Meanly and Webb 1963).

One would logically expect more paternal care as opportunities for finding additional mates diminish. Thus we would predict more paternal care in geographical areas where the breeding season is shorter (continental and more northerly sites). Offspring in these geographical regions also have less time to mature to a point where they are likely to survive to the following season. Together, these two factors (less time to find mates and less time for offspring to

mature) both increase the inherent value of the current brood. It should also be noted that males (with smaller harems of females) that do feed their offspring raise more offspring (on average per season) than males (with larger harems) that only mate and protect their habitats (Muldal *et al.* 1986). The care allotted by the male is also reported to be a great contributor to fledgling success (Whittingham 1989, Whittingham and Robertson 1994).

Methods

Red-winged blackbirds were studied in wetlands near Winnipeg, Manitoba over seventeen consecutive field seasons (a 17-year period) by Dr. Scott Forbes and a field crew each year. I participated in field work in 2009.

Study Species

Red-winged blackbirds have a breeding range that spans nearly all of North America (Costa Rica to Alaska, Atlantic to the Pacific Ocean) (AOU Checklist 1983, cited in Whittingham 1989). The Winnipeg population of redwings is considered to be northern and continental (Forbes 2009). The breeding season is short (approximately two months compared to four months of some southern populations), and the mean clutch size (3.92 nestlings) is among the largest reported for any redwing population (Forbes 2009). Clutch size ranges from two to five (exceptionally six or seven, Forbes 2009) with a modal clutch size of four. Most egg laying took place in late May, and most nestlings were observed in a five week span extending from the first week of June to early July. Nest surveys began in May each year and would end in July or early August.

Nest Records and Videography

The number of nests located and surveyed differed across seasons, but on average 278 nests were surveyed (per season) across the 17 years of field work. These nests were followed from the day they were located (usually during nest-building, but sometimes during egg laying or incubation), until the nestlings reached ten days of age (hatching = day one), or were lost to predation, fledging etc. For identification purposes, eggs and nestlings were marked using non-toxic felt markers. Nest surveys were carried out daily (unless there was severe weather) (Forbes 2009).

Throughout these 17 years of field work, video cameras were set up on nests of interest in order to record intricate behaviours carried out by nestlings and parents. Each camera was set up between 0.5 and 1.5 meters from a nest, and the presence of the camera did not appear to cause any long term behavioural changes in the birds in the videos utilized for this thesis. The positioning of the camera usually disturbed the female redwing, but after a short period (between five and fifteen minutes) she would return to the nest and resume her normal feeding and brooding behaviours. More than 280 videos were included in this project which resulted in detailed observations of behaviours at 221 different nests.

Table 1. Characteristics of video data set utilized for analysis

Property		Frequency
Total tapes analyzed		288
Number with Paternal Care		72
Number with cowbird brood parasites		85
Brood age (day)	1	7
	2	19
	3	35
	4	22
	5	40
	6	38
	7	30
	8	36
	9	45
	10	13
	11	2
Year	1993	26
	1994	36
	1995	19
	1996	65
	1997	64
	1998	2
	1999	0
	2000	0
	2001	0
	2002	0
	2003	2
	2004	10
	2005	2
	2006	6
	2007	6
	2008	37
	2009	13

To prevent pseudoreplication (Hurlbert 1984) no more than one video session per nest was used for analysis. For those nests where more than one videotaping session was conducted, tapes were selected to balance the age distribution (broods ranged from one to ten days of age) in the sample. The duration of video observation in a taping session ranged from just under one hour to over six hours in length (mean length = 3.1 hours). The use of video observations, the sampling of 221 nests, and lengthy observational periods on tape sets this study apart as one of the largest and most detailed collections of data on any wild bird.

Videos were analyzed by Dr. Forbes, myself, and previous field assistants and were scored on the following criteria: year type (good or bad, correlated to weather conditions for prey availability), habitat type (marsh or ditch), time of season, age, size, and structure (number of core and marginal nestlings) of the brood, presence/absence of brown-headed cowbird (brood parasite) nestlings, number of times female fed nestlings, number of times male fed nestlings, and begging intensity of nestlings. Although some videos were scored on all of these criteria, the majority of videos had been previously analyzed without the data on begging intensity. When begging intensity was recorded, it was examined on a scale from zero to four (0 = no movement, 1 = mouth gaping, 2 = neck stretched

and mouth gaping, 3 = standing, neck stretched and mouth gaping, 4 = flapping wings, standing, neck stretched and mouth gaping). When possible, the video scoring was carried out using a blind methodology. A number of the variables (e.g., age of brood, core and marginal status of nestlings, and the presence or absence of a cowbird nestling) were recorded in field journals during the nest surveys and were not combined with the feeding data from the videos until after the scoring was completed.

The total sample of 221 different nests was used to examine the relationships between paternal care and brood size, age, and structure, habitat type, year type, time of season, and the presence of a brood parasite. The effect of male feeding rate on female feeding rate was also recorded to address the question of partial compensation. Smaller samples taken from the 221 nests were used to examine paternal care in relation to the begging intensity.

Statistical Analysis and Modelling

Statistical analysis was carried out using SPSS. Independent variables for full models were selected using *a priori* considerations. A best-fit model was obtained by deleting non-significant variants except for a small number of variables that were of especial interest (year type, and the number of core, marginal, and cowbird nestlings). Logistic regressions were conducted to

determine initial relationships by presenting paternal feeding as a binary variable of 1 or 0 (paternal feeding being present or not present). Multiple linear regression was used to determine to what extent certain characteristics of the brood or the environment affected the rate of male feedings at nests where paternal care was recorded at discernable level.

Results

Paternal care

The presence of paternal care was most closely associated with nestling age. Nests that contained older nestlings were fed significantly more by males than those with young nestlings. Paternal care was present in more than 50% of nests surveyed with nestlings day eight or older (hatching = day one). Habitat type (traditional marsh or ditch) also affected paternal care. Males in ditches fed more than males in marshes. A higher number of core offspring increased the prevalence of paternal care. Large broods commonly received paternal care. The number of cowbird nestlings affected whether or not males fed nestlings in an almost significant manner. The year type and the number of marginal chicks did not significantly affect the occurrence of paternal care (Table 2).

Where males did feed a brood, the feeding rate was affected by a number of variables. The number of core nestlings had the most dramatic effect on feeding rate; males fed at a higher rate when the core brood was large (Tables 3, 4). Male feeding rate was also higher in older broods. The number of marginal and cowbird nestlings, the rate of female provisioning, the habitat type, and the day of season did not influence male feeding rate in a significant manner (Table 3).

Table 2. Results of logistic regression analysis of the relationship between the presence of paternal care; and year type, habitat type, nestling age, and the number of core, marginal, redwing, and cowbird nestlings in a sample of 220 red-winged blackbird nests videotaped at breeding areas near Winnipeg, Manitoba between 1993 and 2009. The full and best-fit regression models are shown.

Independent Variable	**B**	**s.e.**	**Wald Statistic**	**P**
Full Model				
Year Type	0.373	0.378	0.977	0.323
Habitat Type	-0.838	0.367	5.218	0.022
Nestling Age	0.318	0.075	17.907	0.000
Number of Core Nestlings	0.581	0.233	6.214	0.013
Number of Marginal Nestlings	0.236	0.210	1.272	0.259
Number of Cowbird Nestlings	0.563	0.299	3.551	0.060
Constant	-4.312	0.906	22.664	0.000
Best-fit Model				
Year Type	0.370	0.375	0.973	0.324
Habitat Type	-0.803	0.362	4.921	0.027
Nestling Age	0.321	0.075	18.267	0.000
Number of Red-wing Nestlings	0.379	0.182	4.336	0.037
Number of Cowbird Nestlings	0.543	0.296	3.365	0.067
Constant	-4.127	0.890	21.521	0.000

s.e. = standard error, P = significance

Table 3. Results of multiple linear regression analysis of the relationship between male feeding rate of the brood (feedings/hour); and day of season, nestling age, female feedings per hour, habitat type, and the number of core, marginal, and cowbird nestlings in a sample of 70 red-winged blackbird nests videotaped at breeding areas near Winnipeg, Manitoba between 1993 and 2009. The full and best-fit regression models are shown.

Independent Variable	**β**	**s.e.**	**T**	**P**
Full Model				
Constant	-----	2.541	-2.036	0.046
Day of Season	0.078	0.062	0.640	0.542
Nestling Age	0.284	0.215	2.391	0.020
Number of Core Nestlings	0.475	0.462	3.761	0.000
Number of Marginal Nestlings	0.233	0.497	1.742	0.086
Number of Cowbird Nestlings	0.215	0.583	1.598	0.115
Female Feeds per Hour	-0.106	0.057	-0.901	0.371
Habitat Type	-0.014	0.788	-0.114	0.910
Best-fit Model				
Constant	-----	2.102	-2.350	0.022
Nestling Age	0.302	0.202	2.694	0.009
Number of Core Nestlings	0.460	0.453	3.719	0.000
Number of Marginal Nestlings	0.206	0.469	1.634	0.107
Number of Cowbird Nestlings	0.202	0.542	1.619	0.110

FM = (R^2_{adj} = 0.156; $F_{7,63}$=2.853, P=0.012) BfM = (R^2_{adj} = 0.172; $F_{5,66}$=4.640, P=0.002)

s.e. = standard error, P = significance

Table 4. Results of a full model multiple linear regression analysis of female feeding rate (feedings/hour) and results of a full model multiple linear regression analysis of male feeding rate (feedings/hour), both of which examine the relationship between feeding rate (female or male); and day of season, nestling age, proportion of nestlings begging, and the number of core, marginal, and cowbird nestlings in a sample of 81 red-winged blackbird nests videotaped at breeding areas near Winnipeg, Manitoba between 1993 and 2009

Independent Variable	**β**	**s.e.**	**T**	**P**
Full Model (Female)				
Constant	-----	5.797	0.811	0.420
Day of Season	-0.090	0.078	-0.800	0.426
Nestling Age	0.078	0.255	0.679	0.499
Number of Core Nestlings	0.172	0.662	1.422	0.159
Number of Marginal Nestlings	0.286	0.649	2.300	0.024
Number of Cowbird Nestlings	0.014	0.712	0.116	0.908
Proportion of Nestlings Begging	0.057	5.105	0.469	0.641
Full Model (Male)				
Constant	-----	3.753	-1.043	0.300
Day of Season	0.199	0.051	1.798	0.076
Nestling Age	0.139	0.165	1.242	0.218
Number of Core Nestlings	0.376	0.429	3.187	0.002
Number of Marginal Nestlings	0.108	0.421	0.886	0.379
Number of Cowbird Nestlings	0.112	0.461	0.927	0.357
Proportion of Nestlings Begging	-0.033	3.305	-0.276	0.783

FM(Female) = (R^2_{adj} = 0.063; $F_{6,75}$=1.913, P=0.090), FM(Male) = (R^2_{adj} = 0.107; $F_{6,75}$=2.621, P=0.023)

Maternal care

In the facultative biparental care exhibited by red-winged blackbirds, the female plays an obligate role in raising the brood. Maternal feedings are ubiquitous in all studied populations, but the feeding rate can vary. The same variables that I examined for male feeding rate were also examined for female feeding rate. Nestling age was the only variable that produced the same effect between males and females; older nestlings were fed at a higher rate by their mothers as well (Table 5). The number of marginal nestlings increased female feeding rates, but the number of core nestlings did not (in a statistically significant manner) (Tables 4, 5). As the season neared its end, females fed nestlings significantly less, but the parameter estimates are not robust (Tables 4, 5). The begging intensity of nestlings and the number of cowbird nestlings had no significant effect on female feeding rate (Tables 4, 5). Habitat type also had no statistically significant effect on the rate at which the female fed her nestlings. Perhaps most interestingly, the presence of paternal feedings had no discernable effect on the female feeding rate (Table 5).

Table 5. Results of multiple linear regression analysis of the relationship between female feeding rate of the brood (feedings/hour); and day of season, habitat type, nestling age, presence of paternal care, and the number of core, marginal, and cowbird nestlings in a sample of 219 red-winged blackbird nests videotaped at breeding areas near Winnipeg, Manitoba between 1993 and 2009. The results for full and best-fit regression models are shown.

Independent Variable	**β**	**s.e.**	**T**	**P**
Full Model				
Constant	-----	1.865	3.782	0.000
Number of Core Nestlings	0.115	0.446	1.604	0.110
Number of Marginal Nestlings	0.174	0.401	2.523	0.012
Nestling Age	0.312	0.145	4.295	0.000
Day of Season	-0.188	0.050	-2.611	0.010
Number of Cowbird Nestlings	0.049	0.624	0.676	0.500
Presence of Paternal Care	0.001	0.829	0.014	0.989
Habitat Type	-0.028	0.787	-0.393	0.694
Best-fit Model				
Constant	-----	1.572	4.460	0.000
Number of Core Nestlings	0.099	0.441	1.455	0.147
Number of Marginal Nestlings	0.162	0.389	2.411	0.017
Nestling Age	0.304	0.137	4.343	0.000
Day of Season	-0.183	0.049	-2.629	0.009

FM = (R^2_{adj} = 0.098; $F_{6,213}$=4.959, P«0.001), BfM = (R^2_{adj} = 0.094; $F_{4,215}$=7.303, P«0.001)
s.e. = standard error, P = significance

Total (maternal and paternal) feeding rate

The overall feeding rate was highest in older broods. Marginal offspring increased the combined feeding rate slightly more than core offspring (Tables 6, 7). Overall feeding rate to the brood decreased later in the season (Tables 6, 7). There was no discernable effect of nestling begging on the overall feeding rate to the brood (Table 7). Paternal care was associated, not surprisingly, with a higher overall feeding rate (Tables 6, 7). Year type (good/bad), habitat type, and the presence/number of brood parasites were found to have no significant effect on the rate of combined feeding (Tables 6, 7). It should be noted that when begging variables were included in any model (total, maternal, or paternal care) it greatly reduced the significance of the effect of nesting age on provisioning (Tables 4, 7).

Table 6. Results of multiple linear regression analysis of the relationship between total feeding rate (feedings/hour); and year type, day of season, habitat type, nestling age, the presence of paternal care, and the number of core, marginal, and cowbird nestlings in a sample of 219 red-winged blackbird nests videotaped at breeding areas near Winnipeg, Manitoba between 1993 and 2009. The full and best-fit regression models are shown.

Independent Variable	**β**	**s.e.**	**T**	**P**
Full Model				
Constant	-----	1.885	3.015	0.003
Year Type	-0.013	0.750	-0.193	0.847
Day of Season	-0.136	0.051	-1.991	0.048
Habitat Type	-0.032	0.795	-0.484	0.629
Nestling Age	0.304	0.147	4.432	0.000
Number of Core Nestlings	0.158	0.470	2.334	0.021
Number of Marginal Nestlings	0.189	0.405	2.901	0.004
Number of Cowbird Nestlings	0.043	0.653	0.608	0.554
Presence of Paternal Care	0.241	0.838	3.648	0.000
Best-fit Model				
Constant	-----	1.593	3.658	0.000
Day of Season	-0.133	0.049	-2.037	0.043
Nestling Age	0.292	0.143	4.380	0.000
Number of Core Nestlings	0.141	0.448	2.189	0.030
Number of Marginal Nestlings	0.177	0.392	2.801	0.006
Presence of Paternal Care	0.254	0.805	4.008	0.000

FM = (R^2_{adj} = 0.197; $F_{8,211}$=7.722, P«0.001), BfM = (R^2_{adj} = 0.205; $F_{5,214}$=12.323, P«0.001)
s.e. = standard error, P = significance

Table 7. Full model multiple linear regression analysis of the relationship between the total feeding rate of the brood (feedings/hour); and day of season, nestling age, proportion of nestlings begging, presence of paternal care, and the number of core, marginal, and cowbird nestlings in a sample of 74 red-winged blackbird nests videotaped at breeding areas near Winnipeg, Manitoba between 1993 and 2009. The full and best-fit regression models are shown.

Independent Variable	**β**	**s.e.**	**t**	**P**
Full Model				
Constant	-----	5.941	-0.113	0.910
Day of Season	0.054	0.080	0.535	0.594
Nestling Age	0.101	0.263	0.980	0.330
Number of Core Nestlings	0.289	0.694	2.624	0.011
Number of Marginal Nestlings	0.324	0.664	2.925	0.005
Number of Cowbird Nestlings	0.013	0.740	0.118	0.906
Proportion of Nestlings Begging	0.065	5.244	0.600	0.550
Presence of Paternal Care	0.309	1.036	3.075	0.003
Best-fit Model				
Constant	-----	1.736	3.066	0.002
Day of Season	-0.131	0.049	-2.002	0.047
Nestling Age	0.302	0.146	4.432	0.000
Number of Core Nestlings	0.154	0.465	2.303	0.022
Number of Marginal Nestlings	0.187	0.402	2.890	0.004
Number of Cowbird Nestlings	0.048	0.604	0.731	0.465
Presence of Paternal Care	0.245	0.822	3.781	0.000

FM = (R^2_{adj} = 0.260; $F_{7,74}$=5.072, P«0.001), BfM = (R^2_{adj} = 0.204; $F_{6,213}$=10.336, P«0.001)

Discussion

Brood Value

By examining the three sets of feeding results obtained in this study (paternal care, maternal care, and total care) the value of the brood can be estimated according to numerous variables. Brood value was clearly linked to paternal care in this system, and it should be noted that the female's role as the obligate parent swayed the results in the total care data set closer to those seen in the maternal care set. At any given nest, the majority of care (feedings included) received by the nestlings will come from their mother. At this point, I will discuss in detail the variables that affected brood value.

Brood Structure – Core and Marginal

Males chose to feed nests with higher numbers of core offspring. They also fed nests with higher numbers of core offspring at higher rates (more feedings/hour) than those with more marginal nestlings. Interestingly, I found that the female appeared to value the marginal offspring more than the core offspring for any given brood. It is quite possible that the female must increase her feeding rate at nests with marginal offspring in order to avoid starving her brood, while males choose to feed core offspring more than marginal as a way to

create superchicks (*sensu* Mock). Unfortunately, the data for which nestlings were fed at each feeding was not analyzed for this paper.

Brood Structure – Size and Age

Earlier researchers (Clotfelter 1997, Westneat 1995, Whittingham 1989) found that brood size and age both play major roles in determining the allocation of maternal and paternal care in red-winged blackbirds. It is easy to correlate both of these variables to a more valuable brood. Older broods are successful broods. Forbes (2009) described the loss of entire broods as common in the studied population. For a brood to come close to the ten to twelve day fledging age, it must survive a number of trials, each of which demonstrate to the male that said brood might be worthy of his invested time and feeding effort. The female feeding rate would also have to increase as the chicks matured in order to continue satiating them. Male, female, and total feeding rates all increase as a brood ages.

Larger broods are also successful broods. The partial loss of numerous broods was recorded across the 17 years of study, and Forbes (2009) recorded that marginal offspring frequently died as they were out-competed by their core nest-mates. The number of viable offspring each female is able to maintain may be a sign of her (and her offsprings') fitness, thereby enticing a male to feed a

larger brood over a smaller one. Forbes' Winnipeg area results from his 2009 paper showed that nests with higher numbers of offspring fledged the most nestlings. Clutches of five appear to be the optimal size for this population of redwings. It is quite possible that from the male's perspective, bringing food items to one nest containing three to five offspring is an easier (and more attractive) option than making numerous trips between a group of nests with one or two nestlings each. It is interesting however, that the male doesn't seem to be concerned about having all of his eggs in one basket (so to speak), since it is likely that nests with larger numbers of offspring would be more attractive to predators as well. As for the female and total feeding rates, it is quite obvious that for a brood to survive, the feeding rate needs to increase with brood size, just as it did with nestling age.

Habitat

The two habitat types that were studied in detail were the traditional marsh and ditch habitats. It was found that males in ditches were more likely to feed their nests than males in marshes. It is possible that this choice was affected by a differing value of the brood on these two territories. A traditional marsh habitat gave males an approximately circular area on which to amass a harem of females, while the ditch habitat gave a linear range that was functionally smaller.

The cattails used by redwings to build their nests were only available down the centre of a ditch, and if you assume that any given male could hold vigil over x meters in any direction, he would have a much larger useable habitat in a traditional marsh. One potential downside to the traditional marsh set up is seen when examining the effects of cuckoldry on brood value.

In redwings, between one third and one quarter of all nestlings result from extra-pair copulations (EPC's) between a female, and (most commonly) a male from a bordering territory (Westneat 1993, Weatherhead 1993). It is possible that since males in marshes can have numerous neighbours, while males in ditches can only have one neighbour at each end of their linear territory, ditch males have higher confidence in the paternity of their brood. A higher confidence of paternity obviously affects brood value to a male as it increases the payoff for paternal care. If a marsh male's females choose to be promiscuous, and the male invests heavily in a brood containing another male's offspring, he is at a fitness loss. Since the male in the marsh has the potential for numerous neighbours on many bordering territories, he may devalue all of his broods and choose to feed fewer nests. Westneat (1993) reported fewer EPC's in larger harems, although the result did not quite reach formal significance.

Presence of a Brood Parasite

The presence of the brood parasitic cowbird nestling had little effect on any of the three sets of feeding results (paternal, maternal, or total). It was very weakly correlated to the presence of paternal care and all subsequent data analyses produced less significant results. This is an interesting finding when compared to previous research on redwings affected by brood parasites. Clotfelter (1997) found that the red-winged blackbirds don't know that they have been parasitized. If this is true, why then would an additional cowbird nestling not have a feeding rate correlation which more closely resembled that of a marginal nestling? The total feeding rate increased significantly with core and marginal offspring, but showed no correlation to the presence of cowbird nestlings. The female feeding rate increased significantly with marginal offspring, but showed no correlation to the presence of cowbird nestlings. The paternal feeding rate increased with the number of core offspring, but again, showed no significant increase with the presence of a cowbird.

Although none of the probabilities were under 0.05, all of the trends suggested that the cowbird had a positive (instead of negative) effect on the care elicited. It is quite obvious that feeding a genetically dissimilar cowbird nestling offers no initial fitness benefit, and Hauber found that it can also reduce the

parents' future reproductive potential due to energy expenditure (2006). If the redwings were able to determine that one of their nestlings was a cowbird and feed it less, a negative result would be expected. Even still, I feel that the cowbird data certainly brings about more questions than it answers, and it will be interesting in the future when there is time to analyze the "which nestlings were fed at each feeding" and "how much food was each nestling given" variables to see if Clotfelter and other previous researchers may have underestimated the redwings' ability to determine when a nest contains an obligate brood parasite.

Mating Opportunities

Time of Season

An interesting result was found when the time of season variable was examined. Both maternal and total feeding rates fell later in the season (a result that parallels the findings of Yasukawa *et al.* 1989), however, when paternal feeding rate was examined, the opposite was found to be true. As the season neared its end, males did not change their rate of provisioning. As discussed earlier, the female's obligate roll gives her data more influence over the total rate of provisioning data set, but the question as to why females feed less and males continue to feed at the same level as the breeding season progresses should be addressed.

Males presumably have fewer new mating opportunities as the breeding season winds down. Any females that were unmated earlier in the season would probably be mated near the end, and even if a male were to obtain a new mate, it is unlikely that any resulting offspring would survive to the following season (because of their comparatively short opportunity to reach a level of maturity that would see them to the next breeding season). With the knowledge that they stand little chance of mating again and fledging subsequent nestlings, males may prefer to feed any highly valuable remaining broods in an attempt to ensure their success and survival. At the same time, the females may notice their male spending less time looking for new mates while continuing to feed their brood. Females work diligently to raise a brood, and if the above is true, they may succumb to their own "selfish gene" and take a well earned break near the end of the season after being the obligate (often sole) contributor to the success of said brood for the majority of the summer.

Habitat

As discussed in the *Brood Value* section, paternal care was affected by habitat type with a higher prevalence of paternal care in the ditch habitat. An additional (although not mutually exclusive) hypothesis for this result stems from territory size and nest density. Red-winged blackbirds nesting in ditches

were reported to have the lowest nest density of all habitat types (Vierling 1999). If females choose to nest at a low density, it reduces a male's opportunity to attract additional mates and it would be beneficial for a male to feed the current brood in this case.

In terms of territory size, the traditional marsh has much more functional habitat than the linear ditch. More useable habitat could potentially attract a larger harem of females, which would in turn build more nests, which could contain more offspring. Each potentially successful nest on a territory reduces the value of the brood in each nest on that territory, so if a given marsh male was able to hold a larger harem (based solely on his functional territory size) he would have more mating opportunities and feed his nestlings less than a male in a ditch with a smaller harem. The problem with this logic appears in the surprising result from Vierling's (1999) research in Colorado, which found that harem sizes were not significantly different across a number of habitat types. To determine which of these hypotheses (if any) are contributing to this discrepancy in paternal care between habitat types, Dr. Forbes and I plan to examine harem size (through observation) and the paternity of nestlings (using DNA testing) in our population of marsh and ditch nesting redwings in the coming field seasons.

Although males were more likely to feed nests on ditch territories that were examined over the course of this study, it was found that male feeding rate to these nests did not vary when compared to males feeding nests in the traditional marsh territories. Total feeding rate did not differ between marshes and ditches, nor did the female feeding rate. Once again, since the female plays the obligate role in this facultative biparental system, her rate of provisioning remains fairly constant.

Does male help affect female workload?

Previous research suggested that male feedings had little effect on the behaviour of the obligate female. Muldal *et al.* (1986) and Yasukawa *et al.* (1989) found that females did not change their feeding rate when male care was present versus when it was absent. The results from this Winnipeg data set suggest the same. Female feeding rate was not affected in any significant manner by the presence of a feeding male. This result illustrates that any feedings which are allocated by a male are additional to those which the female would have brought her nestlings regardless of his behaviours. If a female were to respond to male provisioning at her nest by reducing her own feeding rate, the male would likely reduce his feeding rate as well, and it is possible that paternal care would not be present in this species at all. As the results demonstrate, any time a male chooses

to feed a brood instead of advertising for further mates, he is giving those nestlings an additional serving of nutrients which is a direct fitness benefit for the nestlings and for himself (as long as they are genetically his nestlings, of course).

An interesting result was found in Mock *et al.*, a study of male care in house sparrows (2004). When nestlings were experimentally subsidized, females continued to feed at their high rate, while males increased their rate of feeding by over 15%. This shows that males (in house sparrows at least) respond to the condition of their offspring and are more than willing to invest into those that already have a high chance of survival. Males in biparental species are likely more interested in creating superchicks than ensuring a high number of offspring survive (a quality over quantity trade-off where the rich get richer).

Does begging intensity affect paternal care?

One final, somewhat surprising, result was that begging intensity and proportion of nestlings begging had no significant effect on the female, male, or total feeding rate. Begging is a very common behaviour for red-winged blackbirds. Whenever a parent perches on the nest the entire brood will take notice and, depending upon nestlings' individual hunger levels, beg with varying intensity. If begging were to have no effect on parental provisioning behaviours it would not remain in the nestlings' behaviour sets because of its

relatively high energetic cost. It is likely therefore, that parents respond individually to the nestlings that are begging hardest per feeding event, but take no indication of the total hunger level of the brood by the amount of begging carried out at any one feeding event. It is also possible that the female is always provisioning near her maximum rate, and so, cannot respond accordingly to any increased begging. Seeing her nestlings beg harder may suggest that they are starving, but there may be little she can do if she is already near her maximum energy expenditure herself.

This raises the question as to why heightened levels of paternal care do not appear to be elicited by a begging brood since it is obvious that the male is rarely provisioning nestlings at his maximum rate. Evolutionarily speaking, if a given male were to respond to a begging brood by attempting to feed them until they were satiated, said male could feed the brood at approximately the same rate as a female for days on end. During these valuable days however, the male would have neglected his other duties. Other females of his harem would have likely been lured onto territories of neighbouring males for extra pair copulations, other nestlings could starve to death without his attention, and predators may have eaten eggs and chicks that were no longer protected. Under these circumstances we would see the value of our male's other broods plummet.

He would be forced to continue to care only for the brood that he had already fed (being that they were still alive, and he could be somewhat confident of their paternity). We can hypothesize therefore, that if a given male were to respond too strongly to the begging of any one brood, he would be setting himself up to become forced into practicing a form of monogamous obligate biparental care.

Conclusions

1. Paternal care in red-winged blackbirds is affected by the interplay between the potential opportunity for a male to attract subsequent mates, and the value of his current brood.

2. The geographic location (northerly and continental) of this Winnipeg population provides a short breeding season with presumably fewer mating opportunities compared to populations in warmer regions; this could explain why males in this population displayed high levels of paternal care (feeding over 50% of their nests that contained nestlings day eight or older) across the 17 year study.

3. Males preferentially fed more valuable broods, which included those with a high number of core offspring, those that were large, and those that contained older nestlings.

4. Paternal care was more prevalent in ditch habitats when compared to marsh habitats, likely due to a higher confidence in paternity, a smaller number of nests, or fewer opportunities to attract females to the ditch habitat.

5. When feeding rate was examined it was found that males fed older broods and broods with a high number of core offspring at a higher rate.

6. The presence of male feedings had no significant effect on the provisioning rate of the female, although the female did feed nestlings less near season end.

7. Since the female provisioning was unaffected by the presence of paternal care, broods that received feedings from their father received additional feedings (and a distinct fitness advantage) when compared to those where the mother was the sole provider.

8. The begging behaviours of nestlings in this study did not elicit more paternal care or a higher rate of provisioning from either parent.

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