ENERGY EXPENDITURE IN REPRODUCTIVE EFFORT OF MALE AND FEMALE KILLDEER *(CHARADRIUS VOCIFERUS)*

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ABSTRACT.—The reproductive investment strategies of the sexes during the breeding season are detailed for Killdeer (*Charadrius vociferus*), a monogamous plover. I measured the energy investments of the sexes in reproductive, mating, and parental effort. As predicted, males expend more mating effort than females; however, the sexes expend equal amounts of parental effort. Total energy expenditure in reproductive effort (mating and parental effort) during a successful nesting attempt was also equal for the sexes. However, early parental effort expenditures by females, early mating effort expenditures by males, and high rates of nest failure combine to result in female reproductive energy expenditures being significantly higher over the breeding season. This suggests that energy expenditure alone is not adequate for accurate comparisons of the relative investments of the sexes. Studies investigating male and female investments need to consider the degree and pattern of nest failures along with patterns of energy expenditure.

The advantages to male and female Killdeer of sharing parental care is demonstrated using adult removal experiments. In general, a deserted parent expends more energy in parental effort than a bi-parental parent and has significantly lower reproductive success. However, males are able to hatch chicks, whereas females lose or abandon their nests within a few days of mate removal. Thus, monogamy in Killdeer appears to result from high nest failure rates, the necessity of two parents for any reproductive success, and the generalizable nature of Killdeer parental care. *Received 30 October 1987, accepted 11 April 1988.*

ALL activities performed by an individual can be classified into either somatic effort, i.e. the time, energy, and risks involved in growth and maintenance activities, or reproductive effort, i.e. the time and energy (Fisher 1958), and risks (Williams 1966, Trivers 1972, Hirschfield and Tinkle 1975, Brunton 1986) incurred in reproduction. Reproductive effort can be divided further into mating effort, activities used to secure copulations, and parental effort, the sum of parental investments in each offspring (Trivers 1972) for a given period (Low 1978, Alexander and Borgia 1979).

An important difference between mating and parental effort is that parental effort is tied to specific offspring whereas mating effort is more general (Low 1978, Alexander and Borgia 1979). Females are able to maintain greater control over their expenditures in parental effort (e.g. egg size, clutch size and number of clutches produced) and benefits from parental effort tend to be greater for females. Males have less control and greater uncertainty of paternity, thus, potentially lower benefits from parental effort. Also, sperm are smaller than eggs and represent a much smaller proportion of an individual's total reproductive potential. The resulting predictions are that females will tend to invest more than males in the parental effort, including egg production, for any given clutch and males will tend to invest more than females in mating effort.

I compared the energy expenditure strategies of male and female Killdeer (*Charadrius vociferus*) in relation to the adaptive value of bi-parental care and monogamy for shorebirds. Killdeer are common North American shorebirds that inhabit a wide variety of open-land habitats. Killdeer are monomorphic, and both sexes are equally capable of providing care for the precocial young (Furniss 1933, Bunni 1959, Phillips 1972, Lenington 1980, Mundahl 1982, Brunton 1988). Chicks leave the nest within 24 h of hatching and are never fed by their parents. Parents lead chicks to feeding areas where both feed on small invertebrates (Furniss 1933, Bunni 1959). Killdeer are multiple brooding; pairs

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remain together throughout the breeding season, and renest after chicks fledge or a nest fails (Brunton 1987). Desertion of second clutches by females has been reported among some populations (Bunni 1959, Lenington 1980, Mundahl 1982), but is absent in others (Brunton 1987).

Few studies have measured the advantages of monogamy by rigorous examination and comparison of male and female reproductive strategies. To measure reproductive effort over the wide range of reproductive activities and the problem of expressing these activities in a common currency is difficult. However, for the different activities involved in reproduction, comparisons can be made between males and females.

I tested 4 predictions: First, the pattern of energy expenditure over a nesting attempt will be different for males and females, with females investing early in egg production. Second, males expend more energy in mating effort and females expend more energy in parental effort. Third, males and females spend similar amounts of energy in reproductive effort (Alexander and Borgia 1979). Fourth, mate removal will result in increased energy expenditure by the "deserted" parent.

Predictions were tested by detailing the daily activities of Killdeer and comparing the relative energy expenditures of the sexes during each stage of the nesting cycle. Cumulative energy expenditures of the sexes were compared during a single nesting attempt and over the entire breeding season. To assess the possible advantages of bi-parental care, I removed adults and compared the energy expenditures of deserted birds with those of bi-parental birds.

METHODS

POPULATION AND STUDY AREA

Field studies began near Ann Arbor, Washtenaw County, Michigan, from April–August 1983. In 1984 and 1985 study areas were located on state- and county-owned lands in the Houghton Lake area of Michigan (lat. 44°02′, long. 08°45′) where all intensive field studies were conducted. Houghton Lake study areas consisted of 3 waste-water treatment plants of 160, 100, and 60 ha, two gravel pits of approximately 15 and 10 ha, and 20 ha of farmland. All sites were sparsely vegetated and contained permanent bodies of water.

Observations began when Killdeer arrived on the breeding grounds in early April. All time-energy budget observations were made on individuals identifiable by dyed plumage, color bands, or unique plumage characteristics. Thirty-seven males (18 in 1984 and 19 in 1985) and 27 females (12 in 1984 and 15 in 1985) were captured on their nests and uniquely color-banded. Nest progress was monitored from discovery until chicks fledged or the nest failed. A reproductive attempt was considered successful if at least one chick fledged.

Behavioral categories.—Killdeer behavior was categorized as somatic or reproductive, including mating and parental effort (Table 1). Somatic effort included all activities that could not be attributed to reproduction. Reproductive effort included all activities involved in reproduction. Division of reproductive activities into either mating or parental effort was based on the apparent purpose of the behavior. For Killdeer, mating effort included behavior that potentially attracts mates (e.g. nest scraping and advertising, copulation, territory establishment and defense). All reproductive activities (except egg formation) performed prior to egg-laying were considered mating effort. Parental effort included energy spent in producing gametes, providing a territory in which chicks feed, and protecting offspring from predators, conspecifics, and inclement weather.

SAMPLING PROCEDURE

Nesting attempts were divided into 6 stages: *Prelaying,* pair formation and arrival on the breeding grounds (mean = 10 days); *Egg-laying,* first egg laid to clutch completion (mean = 6 days); *Incubation,* divided into early, 1–12 days after clutch completion, and late, 12 days after clutch completion until hatching (mean = 24 days); and *Chick Dependence,* divided into brooding, 1–15 days, and post-brooding, 15 days until fledging (mean = 34 days).

Observation samples were 3 h during each of 4 daily time periods (approximately 0500–0900, 0900–1300, 1300–1700, and 1700–approximately 2100). However, some samples were shorter due to occasional, uncontrollable disturbances. Sample periods shorter than 2 h were excluded from the analysis. All Killdeer with active nests were sampled systematically and occasionally individuals were sampled for 6 h consecutively (2 samples in different time periods). Because of high percentage of nest failures (48%; Brunton 1988) not all Killdeer were sampled during all time periods or all nesting stages.

Time budgets were calculated in terms of the percentage of time individuals spent in each of 24 activities (Brunton 1988). Time budgets were measured using 10-s instantaneous sampling of focal individuals. At one study site it was possible to constantly observe both individuals of a pair, and time budgets were collected simultaneously (5 pairs, 82 h). These individuals were treated as separate in the systematic sampling. Time budget data of 42 adults were combined from 1983, 1984, and 1985 and categorized by

TABLE 1. Killdeer activities in categories of effort and estimates of the energetic cost of each activity as a multiple of basal metabolic rate (BMR = 55.2 kJ/day). The sources used measure energy expenditure in laboratory studies unless otherwise indicated.

Activity	Multiple of BMR	kJ/h	Source
	SOMATIC EFFORT (i)		
1 Rest	0.25	0.6	MacMillen, et al. 1977
2 Sitting	0.25	0.6	MacMillen, et al. 1977
3 Standing	0.75	1.7	Bryant, et al. 1985
4 Preening	1.7	3.5	Wooley and Owen 1978
5 Walking	1.7	3.5	Wooley and Owen 1978
6 Foraging	2.0	4.6	Orians, 1961*
7 Running	2.0	4.6	Fedak, et al. 1974
8 Flight	7.0	32.2	Kendeigh, et al. 1977†
	REPRODUCTIVE EFFORT		
MATING EFFORT (j)			
1 Preening display	1.5	3.5	Wooley and Owen 1978
2 Advertising	1.5	3.5	Maxson and Oring 1980*
3 Copulation	1.5	3.5	Maxson and Oring 1980*
4 Nest scraping	1.5	3.5	Maxson and Oring 1980*
5 Nest building	1.5	3.5	Maxson and Oring 1980*
6 Parallel run	1.5	3.5	Maxson and Oring 1980*
7 Courtship chase	1.5	3.5	Maxson and Oring 1980*
8 Flight chase	7.0	32.2	Kendeigh, et al 1977†
PARENTAL EFFORT (k)			
1 Incubation	0.2	0.6	Grant and Whittow 1983
2 Brooding	0.75	1.7	Maxson and Oring 1980*
3 Vigilance	0.75	1.7	Mugaas and King 1981*
4 Leading	1.5	3.5	Fedak et al. 1974
5 Distraction display	1.5	3.5	present study
6 Foraging	2.0	4.6	Orians 1961*
7 Parallel run	2.0	4.6	Fedak et al. 1974
8 Interspecific aggression	2.0	4.6	Maxson and Oring 1980*
9 Flight chase	7.0	32.2	Kendeigh et al. 1977†

* Estimates energy expenditures based on subjective basis.

† Estimates energy expenditure of flight using a regression equation for nonpasserines (excluding aerial feeders) based on laboratory studies of 11 species ranging in size from 3.5 to 1,000 g.

sex, stage of reproduction, time of year, and nesting attempt. Time budgets were calculated excluding data points where birds were out of view; birds were out of view for less than 10% of the sample period.

ENERGY EXPENDITURE MODEL

Estimates of energy expenditures of free-living birds were made by recording time allocation to all activities and multiplying these values by estimated metabolic costs of each activity derived from the literature (Table 1). Energetic costs of activities were expressed as multiples of BMR above the basal level. For example, the cost of brooding involves an expenditure of 0.75 × BMR in addition to a basal metabolism expenditure of 1.0 × BMR.

I assumed that individuals rested (somatic effort) at night except during incubation, when males performed all nocturnal incubation (parental effort), and brooding, when males and females performed equal shares of nocturnal brooding (parental effort) (Brunton 1988). These assumptions were based on 5 nighttime samples where males were found to be incubating, and the observation of predominantly male incubation around sunset.

Daily energy expenditure (DEE) was calculated separately for males and females, for each day, reproductive stage, and breeding season using the energy expenditure model in Eq. 1:

$$\mathrm{DEE} = 24\mathrm{BMR} + H_{\mathrm{B}} + \sum_{\mathrm{i}=1}^{\mathrm{I}} \mathrm{t_i} H_{\mathrm{i}} + \sum_{\mathrm{j}=1}^{\mathrm{J}} \mathrm{t_j} H_{\mathrm{j}} + \sum_{\mathrm{k}=1}^{\mathrm{K}} \mathrm{t_k} H_{\mathrm{k}} + H_{\mathrm{P}}, \qquad (1)$$

where BMR is the basal metabolic rate based on body mass (M) (Ricklefs 1974).

$$\mathrm{BMR} = 0.0808\mathrm{M}^{0.7344}\ (\mathrm{kJ/h}), \qquad (2)$$

where M = 95.5 ± 7.1 g (mean male mass = 94.5 ± 1.0 g, n = 37; mean female mass = 96.8 ± 5.0 g, n =

27; not significant, *t*-test); hence, BMR = 55.17 kJ/day. H_B is the energetic cost of thermoregulation when average ambient temperature (T_i) is below the lower critical temperature (T_{lc}) and is given by:

$$H_B = \sum_{d=1}^{2} t_d \cdot \frac{T_{lc} - T_i}{T_{lc}} \cdot H_{0°C}, \qquad (3)$$

where d = 1, 2 (1 = daytime, 2 = nighttime), t_d = hours (15 h day, 9 h night), T_{lc} = 8°C (Kendeigh et al. 1977), and $H_{0°C}$ = increased metabolic rate at 0°C (Kendeigh et al. 1977).

$$H_{0°C} = 0.4572M^{0.57} \text{ (kJ/h)}, \qquad (4)$$

where t_i, t_j, and t_k are time (h) spent in activities i, j, and k; i, j, and k are somatic, mating, and parental activities, respectively; $H_{i,j,\text{ or }k}$ is the energetic cost of activity i, j, or k expressed in terms of a multiple of BMR above basal level (Table 1); and H_p is energetic costs of gamete production.

Thermoregulation costs (Eq. 3) were calculated from the allometric equations modified for temperature costs of Kendeigh et al. (1977). Early in the season nighttime temperatures regularly went below thermoneutral and only the costs of low temperature were considered. Daily temperatures (minimum, maximum, and temperature at 0700) were recorded throughout the breeding season using readings from the Houghton Lake Meteorological Station at Porter Ranch, Missaukee County, Michigan. When we calculated (3) the average ambient temperature it was between the minimum and 0700 readings for nighttime, and the maximum and 0700 readings for daytime.

The energetic cost of gamete production was considered negligible for males (Ricklefs 1974, Walsberg 1983), but for females it was calculated from the energy analysis of 7 eggs by bomb calorimetry. An oviduct weight of 0.48 g was estimated based on an oviduct/body mass proportion of 0.05 (Rabe 1981). The energetic cost of oviduct development was estimated at 38.0 kJ using an energy density of 8.0 kJ/g (King 1974). Synthesis costs were based on production efficiencies of 77% for egg production and 55% for oviduct production (Drobney 1980). Total egg production costs were 433.8 kJ for a 3-egg clutch and 555.5 kJ for a 4-egg clutch. Egg production costs were divided equally between the pre-laying and egg-laying periods (King 1974, Mugaas and King 1981).

Daily energy expenditure was divided into somatic, mating and parental efforts. Somatic effort included basal metabolic rate, temperature costs and the sum of energy costs of all somatic activities. Mating effort included the sum of energy costs of mating activities. Parental effort included the sum of energy costs of parental activities plus egg production for females. Although somatic activities were assumed to be unrelated to reproductive activities, some reproductive activities have associated maintenance costs and may increase somatic effort (Beissinger 1987). For example, the component of foraging that supports gamete formation and recovery from depletion due to reproductive activities is reproductive effort. This increase in foraging (a somatic activity) should be included in reproductive costs (Alexander and Borgia 1979). Male foraging was considered all somatic effort because they spend the same amount of time foraging during all nesting stages despite different levels of other activities (Brunton 1988). However, females appear to be time constrained and spend significantly more time foraging, with most occurring during pre-laying and egg-laying (Brunton 1988). During pre-laying and egg-laying stages egg production costs are very large and place large energy demands on females. Because male and female Killdeer are monomorphic, their somatic requirements are likely to be the same. Thus, I included the additional time spent foraging by females compared to males during pre-laying and egg-laying in reproductive costs (Table 1). Differences in female foraging time after egg-laying could result from preparation for molt, migration, overwintering or recuperation from current reproduction. A problem only arises if foraging costs are due to recuperation from current offspring. However, recuperation during these later stages is unlikely as the mean weight of females during incubation (24 days) shows no significant increase or decrease (Brunton 1988).

Empirical data are lacking on the energetic costs of the various activities performed by shorebirds in general. These calculations were intended as a means of comparing relative investments of males and females and not as absolute measurements. Modification of this model can be made as data from metabolic studies become available.

Cumulative energy expenditure was calculated for individuals over all reproductive stages by summing the daily energy expenditures for each consecutive stage. To estimate patterns of cumulative energy expenditure, it was necessary to use only data for those individuals observed over the entire nesting period. Suitable data were available for 6 pairs of Killdeer.

If male and female Killdeer have different patterns of energy expenditure in reproduction and there is substantial nest predation, then their average or expected total energy expenditures over a given time period will also be different. I calculated male and female expected energy expenditures as the product of the mean total energy expenditure of a reproductive stage and the proportion of nests surviving to that stage. The expected energy expenditure during early incubation was the total energy expenditure during that stage multiplied by the proportion of nests that survive to that stage (Brunton 1987). By summing these products for all reproductive stages, I estimated the expected cumulative energy expenditure (ECEE) for any nesting attempt.

At Houghton Lake, Killdeer pairs produced an average of 2 clutches per season (Brunton 1987). Estimates of ECEE differed between early (prior to 10 June) and late (after 10 June) nesting attempts. Early

TABLE 2. Daily energy expenditures (kJ/day) by male and female Killdeer during different reproductive stages (mean ± SE).

Reproductive stage	Sex	n	Hours	Daily energy expenditure Somatic	Reproductive	Total
Pre-laying	male	20	82	101.2 ± 8.3	18.6 ± 4.8 *	119.8 ± 16.1 *
	females	18	78	103.1 ± 5.5	39.8 ± 9.8	142.9 ± 9.5
Egg-laying	male	15	42	96.1 ± 15.8	31.2 ± 4.8 *	127.3 ± 13.7 *
	females	14	30	110.3 ± 13.6	62.1 ± 6.7	162.4 ± 2.1
Early incubation	male	23	120	89.6 ± 10.1	17.2 ± 3.6 *	106.8 ± 15.6
	females	19	91	93.3 ± 12.0	7.4 ± 1.9	100.7 ± 10.3
Late incubation	male	14	72	76.7 ± 7.1 *	15.9 ± 2.3 *	92.6 ± 8.1 *
	females	14	68	111.7 ± 8.4	6.9 ± 2.5	118.6 ± 7.3
Brooding	male	12	91	88.3 ± 4.3	21.1 ± 5.1	109.4 ± 9.7
	females	11	83	106.3 ± 11.2	9.5 ± 4.2	115.8 ± 13.4
Post-brooding	male	11	73	106.8 ± 5.9 *	8.6 ± 2.7 *	115.4 ± 12.2
	females	10	67	121.0 ± 12.1	4.9 ± 2.9	125.9 ± 16.1

* $P < 0.05$ (t-test).

nests were more successful than late nests (52%, $n = 70$, compared to 29%, $n = 17$; Chi-square test, $P < 0.05$). All nest failures occurred during incubation, and no pair lost all offspring after hatching. Seasonal ECEE was estimated by adding the ECEE values for early and late nests. Differences between male and female ECEE (early, late, and seasonal) were tested using variances based on the "Law of propagation of errors" (Meyers 1975).

MATE REMOVAL EXPERIMENTS

To assess effects of desertion and single parent care on energy expenditures of deserted individuals, a parent was removed during late incubation, a time when nest desertion has been reported in other populations (Bunni 1959, Lenington 1980). Adults were trapped on the nest and released 30–200 km away from the breeding grounds. Relocated birds did not return to their breeding territories. Three females and 4 males were removed prior to their nests hatching in mid-June 1985. Energy expenditures of deserted individuals were calculated in the same way as those for bi-parental individuals. The number of chicks fledged was used to estimate reproductive success for comparing uni-parental and bi-parental broods.

STATISTICAL TREATMENT

Parametric procedures used included the Student's t-test for 2 independent samples and the Z-test for two individual samples based on the normal distribution. Non-parametric tests were used when sample sizes were small and included the Wilcoxon Rank Sum test for paired samples and the Chi-squared test of independence. A significance level of $\alpha < 0.05$ was used for all tests.

SENSITIVITY ANALYSIS

The division of all activities into categories of effort and then conversion into energy expenditure has a number of problems. Temporal changes in the function of behavior may result in the same behavior being mating effort during pre-laying and parental effort after egg-laying, e.g. territory defense. Therefore, inclusion of some behavior into categories may be more arbitrary than others. Further, the use of time budgets to calculate energy expenditures may involve errors in calculating time spent in activities. However, the greatest potential problem involves uncertainty in the multiplier of an activity and sex differences in time spent in that activity. This type of error could lead to greater differences or similarities than actually exist. Effects of these errors were assessed by varying each multiplier by 25% and examining the impact on male and female differences. In no case did a 25% change in any single multiplier (or all combined) significantly change the relative expenditures of males and females in somatic, mating, parental, or reproductive effort (Brunton 1987).

RESULTS

TEMPORAL PATTERNS OF DAILY ENERGY EXPENDITURE

Female daily energy expenditure (DEE) was significantly greater than male DEE in 3 stages and not significantly different during the other 3 (Table 2). The largest difference between male and female DEE occurred during egg-laying.

Females expended significantly more energy than males in somatic effort during late incubation and post-brooding (Table 2), spending more time foraging (Brunton 1988). Energy ex-

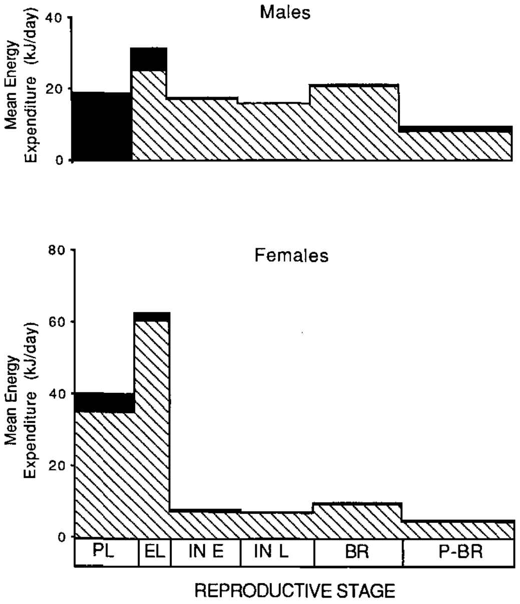

Fig. 1. Mean daily energy expenditure in mating (black area), parental (striped area), and reproductive (total area) effort by males and females for each reproductive stage. Reproductive stages are pre-laying (PL), egg-laying (EL), early and late incubation (IN-E and IN-L), brooding (BR), and post-brooding (P-BR). Male and female sample sizes for each stage are given in Table 2.

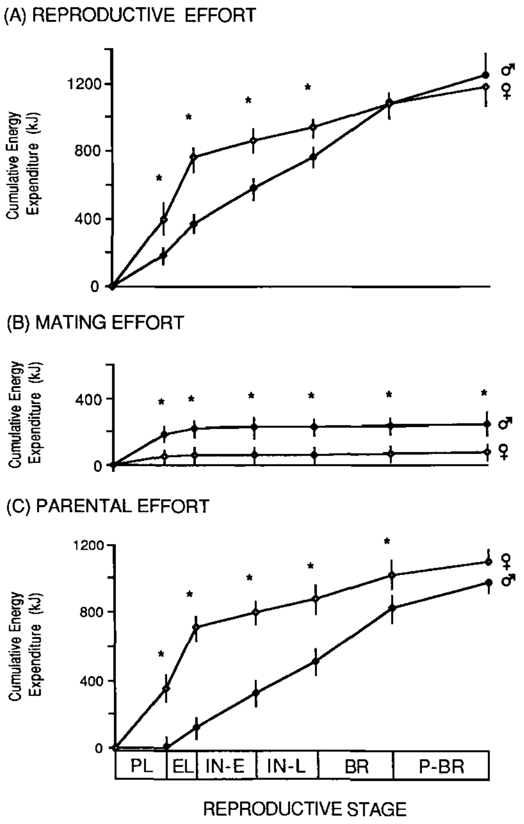

Fig. 2. Cumulative energy expenditure, mean ± SE, in (A) Reproductive Effort, (B) Mating Effort, and (C) Parental Effort by six pairs of Killdeer; males (closed circles) and females (open circles). Reproductive stages are as described in Fig. 1. Asterisk (*) indicates a significant difference between the sexes during a reproductive stage ($P < 0.05$, *t*-test).

penditure in reproductive effort was significantly different for males and females during each reproductive stage (Table 2). Females expended significantly more reproductive effort than males during pre-laying and egg-laying due to egg production costs. Males spent significantly more time incubating and brooding during incubation and chick dependence (Brunton 1988) and have correspondingly higher energy expenditures in reproductive effort. Energy expenditure in reproduction peaked for both sexes during egg-laying. However, the range in reproductive expenditures with stage was greater for females than for males (Table 2).

The allocation of reproductive expenditure to mating and parental efforts also differed between the sexes (Fig. 1). Pre-laying reproductive effort was mating effort for males [mate attraction and territorial defense (Brunton 1988)], but for females it was primarily parental effort in the form of egg production. Expenditure in mating effort was always a small proportion of DEE for both sexes (Table 2). Average mating effort expenditures for males ranged from 0.4 kJ/day during brooding to 18.6 kJ/day during pre-laying. For females, average mating effort ranged from 0.1 kJ/day during late incubation to 4.9 kJ/day during pre-laying. During pre-laying, egg-laying, and late incubation males expended significantly more energy than females in mating effort (*t*-tests, $P < 0.001$; Fig. 1); during all other stages there was no difference between the sexes in mating effort expenditure.

Males expended significantly more mating effort during early nesting attempts (23.9 ± 9.1 kJ/day) than during late attempts (13.2 ± 8.9 kJ/day) (*t*-test, $P < 0.01$) due to the time spent in establishing a territory (Brunton 1988). Female expenditure in mating effort did not differ significantly between early and late nesting at-

TABLE 3. The expected cumulative energy expenditure of males and females throughout the breeding season. Expected values were calculated independently for each stage by multiplying the mean energy expenditure by the proportion of all nests surviving to that stage. The variances were calculated using the law of propagation of errors (Meyers 1975). Expenditures were calculated separately for "early" and "late" nesting attempts; "seasonal" expenditures were calculated by summing "early" and "late" values. For details see Brunton (1987).

Nesting attempt		Expected cumulative energy expenditure (kJ)								
		Mating			Parental			Reproductive		
		Males		Females	Males		Females	Males		Females
Early	$\bar{x}$	237.2	*	68.4	606.7	*	913.5	843.9	*	981.3
	SE	22.1		40.9	54.9		68.1	76.8		82.7
	Ratio		3.5:1			0.7:1			0.9:1	
Late	$\bar{x}$	229.4	*	64.2	400.7	*	818.1	629.1	*	881.8
	SE	32.6		27.6	64.7		77.1	79.6		92.6
	Ratio		3.6:1			0.5:1			0.7:1	
Season	$\bar{x}$	466.6	*	132.7	1,000.7	*	1,741.6	1,474.0	*	1,873.1
	SE	33.4		39.4	79.3		104.4	101.8		122.2
	Ratio		3.5:1			0.6:1			0.8:1	

* Z-test, $P < 0.05$.

tempts presumably because of the relatively minor role in territory defense (Phillips 1972, Mundahl 1982, Brunton 1988). No significant differences existed between early and late nesting attempts for somatic, parental, or reproductive expenditures, or DEE (t-tests; $P > 0.05$).

During pre-laying and egg-laying, females expended more parental effort than males (Fig. 1). This reflected the high cost of egg production which represented a large proportion of female energy expenditure in parental effort (100% and 52%, respectively). However, during incubation and chick dependence, males expended more energy in parental effort than females. Average female expenditures in parental effort ranged from 4.4 kJ/day during pre-laying to 60.3 kJ/day during egg-laying. Average male expenditures in parental effort ranged from 0 kJ/day during pre-laying to 25.5 kJ/day during egg-laying (Fig. 1). Energy expenditure in parental effort decreased as chicks became more independent for both males and females (Fig. 1).

Cumulative energy expenditure in reproductive effort.—Male and female Killdeer showed different patterns of cumulative energy expenditure in reproductive effort (Fig. 2A). Female cumulative reproductive effort (CRE) was significantly greater than male CRE by the end of egg-laying (Fig. 2A). However, male and female CRE did not differ significantly by the end of brooding. The ratio of male to female CRE was 1.1:1 by the end of a successful nesting attempt.

Male cumulative energy expenditure in mating effort (CME) was significantly greater than female CME throughout the nesting attempt (Fig. 2B). The ratio of male to female CME was 3.3:1 by the end of a successful nesting attempt.

Female cumulative energy expenditure in parental effort (CPE) was significantly greater than male CPE from pre-laying until the end of brooding (Fig. 2C). After brooding male expenditure increased more than female expenditure resulting in equal CPE by males and females at the end of a nesting attempt (Fig. 2C). The ratio of male to female CPE was 0.9:1 by the end of a successful nesting attempt.

Expected seasonal energy expenditure.—Male and female expected cumulative energy expenditure (ECEE) in reproductive effort was not significantly different for early nests. Females expended more in late nests and over the season (Table 3). Expected cumulative energy expenditure in mating effort was significantly greater for males than females in early and late nests, and over the season (Table 3). ECEE in parental effort was significantly greater for females than males for early and late nests, and over the season (Table 3).

Mate removal and energy expenditure.—None of the 7 deserted parents raised chicks past brooding. All deserted females lost or abandoned their nests before chicks hatched. Two of the 4 deserted males successfully hatched their broods but both broods were lost within 10 days of hatching.

TABLE 4. A comparison of the energy expenditures (kJ/day) in somatic, mating and parental effort by bi-parental and "deserted" Killdeer during late incubation and brooding (mean ± SE).

Reproductive stage	*n*	Hours	Daily energy expenditure			
				Reproductive		
			Somatic	Mating	Parental	Total
A) Males						
Late incubation						
bi-parental	14	72	76.7 ± 6.3 *	0.3 ± 0.4	15.6 ± 1.8	92.6 ± 8.1 *
deserted	4	46	59.0 ± 3.5	0.1 ± 0.2	16.5 ± 0.4	75.6 ± 3.4
Brooding						
bi-parental	12	91	88.3 ± 4.3 *	0.3 ± 0.4 *	20.0 ± 8.6 *	109.4 ± 9.7
deserted	2	15	62.2 ± 5.4	3.8 ± 1.1	37.5 ± 2.8	103.5 ± 5.7
A) Females						
Late incubation						
bi-parental	14	68	111.7 ± 7.4 *	0.1 ± 0.2	6.8 ± 2.1 *	118.6 ± 9.2 *
deserted	3	22	70.4 ± 6.4	0	11.8 ± 1.3	82.2 ± 3.3

* $P < 0.05$ (t-test).

During late incubation the energy expenditures of deserted males and females were significantly different (t-test, $P > 0.05$). Deserted males expended significantly more energy on parental effort than deserted females (16.5 ± 0.4 and 11.8 ± 1.3 kJ/day, respectively; t-test, $P < 0.01$).

The DEE of deserted males was significantly less than that of bi-parental males during late incubation (Table 4). However, deserted males expended the same amount of energy as bi-parental males in parental effort but less in somatic effort. Deserted and bi-parental males did not expend significantly different amounts of mating effort (Table 4).

A comparison of deserted and bi-parental females during late incubation showed the same pattern. Deserted females spent significantly less energy in somatic effort, more energy in parental effort and less DEE than bi-parental females (Table 4).

Deserted males did not expend significantly more DEE than bi-parental males after chicks hatched (Table 4); however, deserted males expended significantly less than bi-parental males on somatic effort, and more on mating and parental effort.

DISCUSSION

Daily energy expenditures (DEE) of male and female Killdeer varied with stage of reproduction. Highest values of DEE occurred during egg-laying for both sexes. Male expenditure was high due to territorial defense, whereas, female expenditure was high due to egg production. The low energy expenditures of both sexes during incubation was most likely the result of the large amount of time spent incubating (Brunton 1988) and the very low energetic cost of this activity (Ricklefs 1974, Walsberg and King 1978). Ettinger and King (1980) reported little breeding season variation in DEE for male and female Willow Flycatchers (*Empidonax traillii*). They suggested this supported Wilson's "principle of stringency" (1975), i.e. uncommitted time (or energy) serves as a buffer against unpredictable events. In contrast, the DEE of female Killdeer appeared to respond directly to the different demands of each reproductive stage. Male DEE varied less and male time budgets show that males have more "loafing" time (preening, standing) than females (Brunton 1988).

As predicted, patterns of energy expenditure in reproductive, mating and parental efforts over a nesting attempt differed for male and female Killdeer. Females invested substantially in parental effort (eggs) early in nesting, and an initial disparity occurred in energetic investment by the sexes (Trivers 1972, Dawkins and Carlisle 1976). Sexual selection theory predicts that the sex that initially invests most in gametes will be a limiting resource for the sex that invests least (Bateman 1948, Fisher 1958). This often results in intrasexual competition among members of the sex that invests least, in this case males. Investment by males in mating effort has been predicted to reduce this difference (Low 1978, Alexander and Borgia 1979, Gladstone 1979). Killdeer males have invested consider-able energy in reproductive effort at the start of egg-laying. All of this was mating effort, e.g. territorial defense, mate attraction behavior, and nest building (Brunton 1988).

Greater expenditure in mating effort may benefit males more than females because male reproductive success is limited by the number of females he can inseminate, and mating effort may reduce the likelihood of cuckoldry (Alexander and Borgia 1979, Burger 1981). Male Killdeer spent more energy in mating effort and obtained more extra-pair copulations than females (5 and 0, respectively). Female Snail Kites (*Rostrhamus sociabilis*) decreased the disparity by forcing extended, energetically expensive, and non-generalizable investments by males in courtship prior to mating (Beissinger 1987). In Black Skimmers (*Rynchops niger*) territorial defense and courtship feedings result in males investing more in reproductive effort than females prior to egg-laying (Burger 1981). Further, in contrast to the second prediction, the sexes appear to expend roughly equal amounts of energy in parental effort.

The third prediction, that males and females spend equal amounts of energy in reproductive effort (Alexander and Borgia 1979), was supported for successful nesting attempts by Killdeer. However, comparisons of cumulative energy expenditure in a successful nesting attempt may not be representative of the actual reproductive energy expenditures of males and females. Actual energetic expenditures in reproduction will be a result of the length of the season, nest stage(s) at which investments are made, and patterns of nest failure. Estimates of expected seasonal energy expenditure were more representative of the relative investments of the sexes (Ricklefs 1974, Walsberg 1978) and did not support the prediction of equal investment by the sexes in reproductive effort. The ratio of male to female investment dropped from 1.1:1 to 0.8:1.

The effects of nest failures on relative investments of the sexes can be illustrated further by comparing reproductive effort in early and late nesting attempts. Early nests were more successful and expected cumulative expenditures of males and females in reproductive effort were not significantly different. Late nests were much less successful and females expended significantly more than males. This difference resulted from differences in nest failures. Failed nest attempts always preceded hatching, a time when females had invested more than males.

Males showed a seasonal difference in expenditure of mating effort. Early nesting attempts required more energy because of territory establishment and defense. Late nesting attempts did not require large investments unless his mate deserted and a new mate was required. Female mating effort remained relatively constant for successive nests. Successive nesting attempts tended to reduce the disparity between the sexes.

Males of many shorebird species have the more active role in parental care late in the nesting cycle (Parmelee et al. 1968, Bengtson 1970, Graul et al. 1977, Ashkenazie and Safriel 1979, Maxson and Oring 1980, Walters 1982, Miller 1985). The most common explanation for this behavior is high rates of predation which favors a substantial parental role by males, and enables quick renesting by females (Ashkenazie and Safriel 1979, Walters 1982, Evans and Pienkowski 1984). Nest failure among shorebirds is higher during incubation than any other reproductive stage (Evans and Pienkowski 1984). The apparent greater parental role of males among monogamous and polyandrous shorebirds may not necessarily result in greater male than female investment in parental effort or reproductive effort over a season. Energy expenditure alone may not be adequate for comparisons of the relative investments of the sexes. Reports of greater male than female parental roles for monogamous and polyandrous species must consider the extent and pattern of nest failures along with patterns of energy expenditure.

The role of bi-parental care in maximizing male and female fitness is an important assumption of the evolution of avian monogamy (Wittenberger and Tilson 1980). Females are likely to benefit from monogamy and male parental care because their reproductive success is usually limited by time and energy constraints. The removal of a mate is a crucial experimental test of the importance of bi-parental care (Gowaty 1983). It is also a means of assessing the increased energetic cost to the 'deserted' parent of uni-parental care.

Adult-removal experiments of Killdeer supported the prediction that females were unable to successfully raise young alone, and that male assistance greatly enhanced female reproductive success. Deserted parents expended more reproductive effort and less somatic effort than bi-parental parents regardless of their sex. Although no nests were successful, males and females were not equally able to raise young alone. The males hatched chicks but females did not. This was probably due to the more active involvement of males in the defense and maintenance of a territory. Deserted females were unable to maintain their territory and left soon after male removal. Deserted males remained on their territories, and increased their energetic expenditure in mating effort.

Female desertion has been observed in two Killdeer populations (Bunni 1959, Lenington 1980). In the population of Killdeer I studied, mate or nest desertion was rare (3/87 nesting attempts) and usually the result of repeated nest failure (2/3 nesting attempts). One case of polyandry was observed (Brunton 1988). The apparent differences in the frequency of desertion between Killdeer populations may result from different levels of predation. High predation rates may place a premium on good female condition for renesting (Parmelee and Payne 1973, Emlen and Oring 1977, Maxson and Oring 1980).

In Killdeer populations where mates are deserted, females leave late in the season, after chicks hatch (Bunni 1959, Lenington 1980). Alternative strategies for male Killdeer may be less profitable than continued parental care due to costs involved in deserting his mate. Additional mating opportunities are affected by the degree of breeding synchrony in the population (Emlen and Oring 1977) and the operational sex ratio. They were low for male Killdeers as females aggressively excluded other females from their territory (Phillips 1972, Mundahl 1982, Brunton 1987), and not all males holding territories obtained a mate. The most successful strategy for Killdeer males may be to invest in parental care during stages when offspring survival was highest. Further, by remaining with the same mate, males reduced energetic costs of remating and the time involved in renesting (Brunton 1987).

The importance of territorial defense for Killdeer monogamy and bi-parental care may arise from the ability of males to control their confidence of paternity, and because territorial defense is a form of parental care. As in other precocial, monogamous species, male Killdeer invest more in defense than females (Erickson and Zenone 1976, Emlen and Oring 1977, Mundahl 1982, Brunton 1988). Territorial behavior is generalizable and easily changed from parental to mating effort. Therefore, males may maximize fitness by maintaining a territory, and caring for the offspring rather than deserting their mates and establishing a new territory.

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