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THE INFLUENCE OF DIET QUALITY ON CLUTCH SIZE AND LAYING PATTERN IN MALLARDS

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Abstract.—We measured the effect of diet quality on variation in the seasonal pattern of Mallard (*Anas platyrhynchos*) reproduction. Twenty wild-strain hens, consisting of 10 sibling pairs, were maintained in captivity. One sib of each pair was fed an enriched diet, and the other was fed wheat. The wheat diet resulted in reduced clutch size, egg size, laying rate, number of nesting attempts, and total eggs laid. Diet did not affect laying initiation, duration, or the seasonal pattern of change in clutch and egg size with each renest. We believe the variation and pattern observed are adaptations to a highly variable prairie environment where the probability of reproductive success decreases as the season progresses. *Received 20 April 1987, accepted 4 October 1987.*

WILLIAMS (1966) observed that the central biological problem is not survival as such, but design for survival. Inherent in this design is a set of coadapted reproductive traits evolved through natural selection in response to particular ecological problems (Stearns 1976). The traits include variables such as age of first reproduction, clutch size, size of young, pattern of seasonal reproductive investment, and level of reproductive effort.

Variables incorporated in a life-history strategy are commonly assumed to be subject to normalizing selection, and the mean value is considered more indicative of an adaptation than the variance. For example, when a consistent clutch-size pattern is observed, as when the average clutch size is smaller than the most productive, an ultimate, adaptive explanation seems appropriate. But when clutch size varies with environmental changes such as food availability or female condition, proximate explanations are often provided (cf. Klomp 1970, Johnsgard 1973, Winkler and Walters 1983). There is no a priori reason to assume a facultative response to environmental change is proximate or that an obligate response is adaptive (Stearns 1976). For example, female carabid beetles have longer reproductive lives when they facultatively reduce reproductive investment during poor conditions (Murdoch 1966).

Phenotypic plasticity may be important in the evolution of life-history strategies. Ultimate and proximate causation are not necessarily mutually exclusive, and, indeed, food supply may play a dual role (Winkler and Walters 1983, Winkler 1985). Our understanding of the effect of food supply on life-history variation is imperfect. For this reason it is useful to determine in a single species which reproductive traits are flexible and which are fixed in the face of variation in food supply. We considered the effect of diet quality on variation in the seasonal pattern of Mallard (*Anas platyrhynchos*) reproduction. We specifically tested for variation in the timing of laying initiation and duration, total eggs produced, egg size and composition, rate of egg laying, clutch size, interval between clutches, and seasonal clutch-size decline.

METHODS

Mallards were collected as eggs from Audubon National Wildlife Refuge in North Dakota in 1974. Clutch size, egg mass, and egg-size measurements were taken for all wild clutches. Eggs were incubated and ducklings were weighed and raised at Northern Prairie Wildlife Research Center for the experiment, which was conducted from 18 April until 24 June 1975.

Twenty pairs were placed in individual outdoor pens equipped with plastic floor covers to prevent the birds from feeding on extraneous plant or animal matter. The 20 hens consisted of 10 sibling pairs. One sib of each pair was fed an enriched laying diet (28.7%

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TABLE 1.   Influence of diet quality on observed variation in the body mass of 10 sibling pairs of Mallards (20 females).[a]

Source	df	Preseason body mass		Seasonal loss of body mass	
		F	P[b]	F	P[b]
Sib pair	9	0.38	NS	0.49	NS
Diet	1	0.00	NS	0.03	NS

[a] Random block design, testing for sibling pair and for diet effect between sibs within a pair with an F statistic.

[b] NS = no significant difference.

protein), and the other was fed wheat (18.2% protein). All were allowed to feed *ad libitum* and given oyster-shell supplement for calcium. Nest boxes were checked daily, and eggs were labeled as they were found. When a hen quit laying for 3 days her entire clutch was removed. The eggs were weighed and analyzed for yolk mass, percentage of yolk lipids, and moisture content. Lipids were extracted by the Sohxlet procedure using petroleum ether and following the "Official Methods of Analysis" (Assoc. Official Agric. Chem. 1975).

The analyses stratify for sibling pairs in a random block design using an F statistic (Neter and Wasserman 1974). Where appropriate, more extensive split-plot analyses of variance were performed. We used covariance analyses to test for consistent seasonal trends in laying pattern, blocking for sibling pairs, and regressing on the covariate, nesting attempt. All tests were performed with the SAS GLM (General Linear Model) procedure (SAS Inst. 1982).

RESULTS

The body mass of 20 experimental hens averaged 1,077 ± 94 g, a value consistent with those obtained from the wild (Krapu 1981, Cowardin et al. 1985). Hens on different diets did not differ significantly in preseason body mass or loss of body mass during the season (Table 1).

Sibling pairs did not differ significantly in the total number of eggs laid during the season, but hens on the enriched diet laid more eggs than their sibs on wheat (Table 2, Fig. 1a).

Laying rate (eggs/day within a clutch) for all hens averaged 0.8 eggs/day ($n = 49$ clutches, range = 0.4–1.0 eggs/day). Sib pairs differed, but diet also significantly affected laying rate. Hens on wheat laid at a slower rate than their sibs on the enriched diet (Table 2, Fig. 1b). A covariance analysis revealed no significant change in laying rate during the season (Table 3).

Hens renested in an average of 4.7 days after eggs were removed ($n = 34$ intervals, range = 2–24 days). Diet had a significant effect on renesting interval, with hens on wheat requiring more time to renest than their sibs on an enriched diet (Table 2, Fig. 1c). A covariance analysis did not reveal a seasonal trend in renesting interval (Table 3).

The number of clutches initiated by a hen during a season averaged 3 ($n = 20$ hens, range = 1–5 clutches). Diet affected the number of nests attempted; hens on the enriched diet attempted more nests during the season than did their sibs on wheat (Table 2, Fig. 1d).

The date the first egg was laid averaged 2 May ($n = 20$ hens, range = 20 April to 15 May). Laying initiation among sibling pairs differed, but sibs on different diets started laying about the same time (Table 2, Fig. 1e).

On average there were 44 days between first and last egg of the season ($n = 20$ hens, range = 27–62 days). Laying duration among sibling pairs differed, but sibs continued laying for about the same period of time (Table 2, Fig. 1f). We found no relationship between loss of body mass during the season and laying duration, but we found a strong negative relationship between initiation date and duration of laying ($r = -0.95$) (Fig. 2). This relationship was due to birds initiating earlier than the average ini-

TABLE 2.   Influence of diet quality on observed variation in reproductive parameters of 10 sibling pairs of Mallards (20 females).[a]

Source	df	Total eggs		Laying rate		Nest interval		Nest attempts		Initiation		Duration	
		F	P[b]	F	P	F	P	F	P	F	P	F	P
Sib pair	9	2.24	NS	4.01	**	1.19	NS	1.19	NS	3.00	*	3.52	*
Diet	1	56.68	***	25.42	***	7.71	**	16.20	**	2.40	NS	3.73	NS

[a] Random block design, testing for sibling pair and for diet effect between sibs within a pair.

[b] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS = no significant difference ($P > 0.05$).
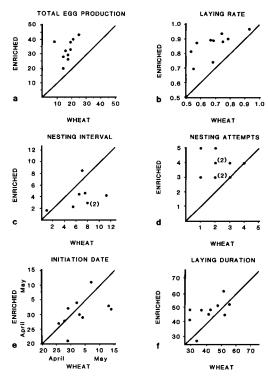
Fig. 1. The influence of diet on total egg production (a), laying rate (b), nesting interval (c), nesting attempts (d), initiation date (e), and laying duration (f). Each point represents 2 sibling hens; one sib was fed an enriched diet, and the other was fed wheat. The analysis tested for consistent differences between sibs illustrated here as trends in where the points fall relative to the isometric diagonal line.

Fig. 2. Relationship between laying duration and initiation date for 20 females.

tiation date and nesting beyond the average date of cessation (variance in initiation dates and time of cessation did not differ significantly using a Hartley comparison of variance, $H = 1.602, r = 2, n = 20$; Neter and Wasserman 1974). The pattern suggests an inherent tendency for some birds to invest more in a single year by beginning earlier and ending later.
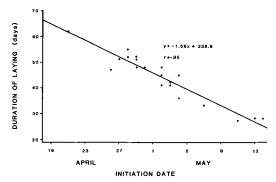
Mallard egg mass was highly variable, ranging from 39.7 to 68.8 g and averaging 53.7 g/egg for 484 eggs. These values were consistent with variation observed in wild eggs (613 eggs we collected from the wild between 1974 and 1981 averaged 52.2 g and ranged from 32.2 to 66.7 g). A split-plot analysis (Table 4) revealed that most of the variation in egg mass was caused by inherent differences among sib pairs, but diet also strongly influenced egg mass; hens on the enriched diet laid heavier eggs. Compared with egg variation explained by diet, differences among nesting attempts were small. A covariance analysis, however, revealed that within sib pairs, eggs increased in mass with each attempt (Table 3). Eggs became, on average, 0.43 g heavier with each successive renest clutch, starting from an initial average of 54.5 g for enriched and 48.4 g for wheat diet. Batt and Prince (1979) also observed heavier eggs in renest clutches, but they did not find a trend within hens.

Because diet significantly affected egg mass, we asked how eggs from natural diets compared with those observed in the experiment. We expanded the analysis to include values from the

TABLE 3. Seasonal change in laying rate, renesting interval, egg mass, clutch size, and clutch mass with each nesting attempt for 10 sibling pairs of Mallards (20 females).[a]

Source	df	Laying rate		Renesting interval		Egg mass		Clutch size		Clutch mass	
		F	P[b]	F	P	F	P	F	P	F	P
Diet	1	23.75	***	5.89	*	278.50	***	11.23	**	17.20	***
Sib pair	9	3.84	***	1.01	NS	12.23	***	0.84	NS	0.89	NS
Nesting attempt	1	0.43	NS	0.08	NS	4.77	*	47.18	***	39.82	***

[a] Covariance analysis testing for diet and for sibling pair effects and regressing on covariate, nesting attempt.
[b] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS = no significant difference ($P > 0.05$).

TABLE 4.   Influence of inherent differences among 10 sibling pairs of Mallards (20 females), diet quality, and sequence of nesting attempt on the observed variation in egg mass, clutch size, and total clutch mass.[a]

		Egg mass		Clutch size		Clutch mass	
Source	df	F	P[b]	F	P	F	P
Sib pair	9	14.49	***	0.64	NS	0.71	NS
Diet	1	8.42	**	5.16	*	12.15	**
Sib pair × diet	9	10.22	***	0.61	NS	0.39	NS
Nesting attempt	3	0.67	NS	10.57	***	8.38	***
Diet × nesting attempt	3	0.14	NS	0.51	NS	0.66	NS

[a] Split-plot design, testing (F statistic) for main effects and interaction for sibling pairs, diet quality, and sequence of nesting attempt.
[b] * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$, NS = no significant difference ($P > 0.05$).

natal clutch of each sib pair collected in the wild. Eggs from these clutches were produced on a natural diet by the wild mother of each sister pair (see Swanson et al. 1985 for the natural diet of laying female Mallards). Egg mass differed significantly among the three members of a family group (random block design, $P = 0.0001$). In most groups the daughter fed an enriched diet laid heavier eggs than either its mother on a natural diet or its sib on wheat, suggesting food may be limited in the wild (Fig. 3). These findings are relevant because egg mass is proportional to duckling mass (Fig. 4), and ducklings from larger, heavier eggs seem to have a better chance of survival than ducklings from small eggs (Kear 1965, Marcstrom 1966, Lack 1967, Krapu 1979).

Dry yolk mass was related to egg mass (yolk dry mass $= -1.35 + 0.225$[egg mass], $P = 0.0001$, $r = 0.84$, $n = 37$ wild eggs), so, not surprisingly, we found a significant difference in dry yolk mass both among sib pairs and between diets (Table 5, Fig. 5). Percentage of moisture also differed among sib pairs and between diets (Table 5, Fig. 5). Percentage of lipids remained relatively constant between sibs on separate diets and among sib pairs (Table 5, Fig. 5). In summary, the size of the yolk, measured as dry yolk mass, and the percentage of dry matter varied among hens and with diet, but the percentage of lipids was relatively constant. These results suggest that, in addition to inherent variability between hens in the amount invested in eggs, egg composition was influenced by diet quality.

Diet had a significant influence on clutch size. Hens on enriched diets laid, on average, 2.6 eggs more than sibs on wheat for all clutches. Regardless of diet, most of the observed variation in clutch size was due to renesting (Table 4: Nest attempt). A covariance analysis revealed a significant decline in clutch size with each

nesting attempt (Table 3) from an initial average clutch of 12 eggs for enriched and 9.5 for wheat diet. A decline is consistent with Batt and Prince's (1979) findings, but the decline they observed was caused by renesting and by a reduction in the size of first clutches laid later in the season. We did not observe a reduction in first-clutch size with time (Fig. 6). The decline in first clutches may have been an artifact of the diverse latitudinal origin of their captive flock (cf. Batt and Prince 1978).

Variation in egg mass and clutch size was reflected in the variation in total clutch mass. A split-plot analysis mirrored the previous results revealing a major influence of diet and nesting attempt (Table 4). Although eggs became slightly heavier in renest clutches, the egg loss with each nesting attempt resulted in a total clutch mass decline during the season (Table 3).

Although clutch size declined during the season, the overall investment of the hen in reproduction increased cumulatively at a decelerating rate (Fig. 7). Birds on enriched diets laid larger eggs, laid them at shorter intervals, renested sooner, and attempted more nests in the face of intense, artificial predation than their sisters on wheat. As a result, the enriched-diet group laid considerably more than their own body mass in eggs, and their laying pattern of cumulative egg mass increased almost linearly with time (Fig. 7). Wheat-diet birds laid fewer, lighter eggs and delayed laying both during and between clutches. Diet did not influence laying initiation or duration, and hens that initiated earlier than average often continued laying after the average date of cessation.

DISCUSSION

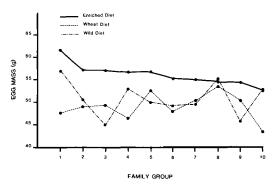Variation in diet quality in captive Mallards significantly affected clutch size, egg mass, egg

Fig. 3. Average egg mass of individual hens from 10 family groups. Each group includes one wild hen and two captive daughters ($n = 30$ females).

Fig. 4. Relationship between duckling and egg mass.

composition, laying rate, renesting interval, nesting attempts, and total eggs laid. There is probably considerable flexibility in response to environmental conditions.

Several reproductive parameters remained relatively constant in spite of diet variation. The birds were relatively consistent in laying initiation and duration. Most renested at least once in response to artificial nest predation. In addition, clutch size declined while egg size increased with renesting. This latter pattern is reminiscent of a general reproductive trade-off in plants and animals between offspring size and number (Williams 1966, Stearns 1976).

We suggest that the flexible response to food quality we observed is adaptive in a highly variable prairie environment, and the consistent patterns in initiation, laying duration, and egg and clutch size are adapted to predictable seasons where habitat conditions deteriorate with time. Our interpretation is consistent with Winkler (1985), who explained clutch-size differences between two populations of gulls as a flexible response to pre-egg environmental conditions.

Precipitation in the midcontinental prairies is highly variable from year to year. This vari-
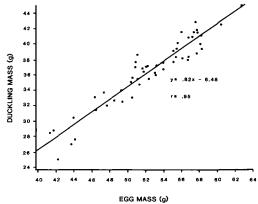
ation is reflected in the number of small ponds available to nesting Mallards (Fig. 8). In spring Mallard hens rely on aquatic invertebrates for food (Swanson et al. 1985), so, presumably, a direct link exists between food and pond availability. They nest near the ponds on the ground, and nest predation is common (Johnson and Sargeant 1977, Sargeant et al. 1984, Cowardin et al. 1985). Many of the ponds that are available in May are consistently dry by July (Fig. 8). As a result, Mallards nest initially in a highly variable environment, but they are forced to renest under consistently deteriorating conditions.
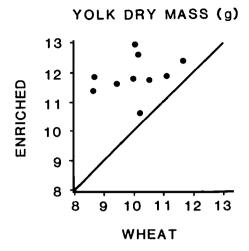
The experimental reproductive flexibility we observed is consistent with that observed in the field. For example, clutch size in wild ducks varies with available food resources (Bengtson 1971), and wild Mallards respond to variation in pond availability by opportunistically settling in breeding habitat in the spring (Johnson 1986), and in dry years they lay smaller clutches (Krapu et al. 1983) and renest fewer times (Cowardin et al. 1985). These results suggest that Mallards are adapted to nest under a wide variety of conditions by adjusting reproductive effort to environmental conditions.
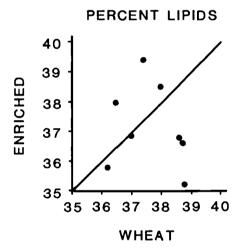
TABLE 5. Influence of diet quality on observed variation in yolk characteristics of 10 sibling pairs of Mallards (20 females).[a]
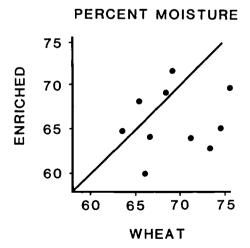
Source	df	Dry yolk mass		% lipids		% moisture	
		F	P	F	P	F	P
Sib pairs	9	7.68	***	1.64	NS	6.43	***
Diet	1	117.37	***	1.08	NS	10.67	***

[a] Random block design testing for sibling pair and for diet effect between siblings within a pair.
[b] *** = $P < 0.001$, NS = no significant difference ($P > 0.05$).

YOLK DRY MASS (g)
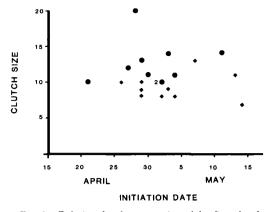

PERCENT LIPIDS

PERCENT MOISTURE

Fig. 6. Relationship between size of the first clutch and initiation date (circle = enriched diet, diamond = wheat diet).

Although prairie weather is highly variable, seasonality itself is generally predictable. In our experiment nest initiation and duration by individual hens did not vary with diet. These results are consistent with Batt and Prince (1979), and they suggest an adaptation to the predictable pattern of seasonality at each latitude (Batt and Prince 1978).

Seasonal deterioration in prairie water conditions is another predictable environmental pattern (Fig. 8). The ponds most used by Mallards are often those most likely to dry during the season (Stewart and Kantrud 1971, 1973; Krapu et al. 1983). We suggest that the decline in renest clutch size and increase in egg size we observed are adaptations to predictable seasonal decrease in the probability of reproductive success caused by deteriorating water conditions.

Charnov and Krebs (1973), expanding on Williams' (1966) original suggestion, proposed a model for clutch-size reduction with increasing adult or juvenile mortality, or both. If this model were modified to include consistent seasonal change, then smaller renest clutches would be predicted if either juvenile or adult mortality increased with time of season. In the prairie environment, both juvenile and adult mortality probably increase during the season.

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Fig. 5. Influence of diet on (a) yolk dry mass, (b) percentage of lipids, and (c) percentage of moisture. Each point represents 2 sibling hens (see Fig. 1).
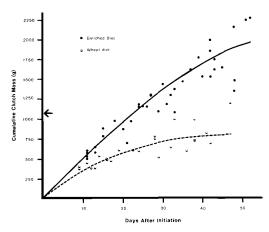
Fig. 7. Summary of the cumulative investment in egg production by experimental hens. The arrow marks the average hen mass at the start of the experiment. The curved lines were drawn by hand to clarify the differences between diet groups.
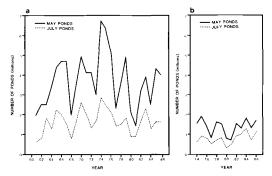

Fig. 8. Variation in the number of ponds in (a) southern Alberta, Saskatchewan, and Manitoba and (b) in Montana, North Dakota, and South Dakota (U.S. Fish Wildl. Serv. and Can. Wildl. Serv. 1986).

Duckling mortality might increase from wetland loss during the season, from increased travel, and from greater predation on very young ducklings. Mallard ducklings are most vulnerable during the first week after hatch, when hens lead them from wetland to wetland searching for an invertebrate food supply (Talent et al. 1983). This period of mobility is an energetic strain, and duckling size may directly influence duckling survival (Kear 1965, Marcstrom 1966, Lack 1968, Krapu 1979). In addition, mink, the major predator on ducklings in the midcontinental region (Sargeant et al. 1973, Eberhardt and Sargeant 1977), produce young at this time, which theoretically increases predator pressure during the season. As a result, the frequency and distance of overland trips and predation risk may be greater for ducklings hatched later in the season. Hammond (unpubl. data) found a greater decline in brood size of week-old ducklings late in the season than expected from clutch-size decline alone.

Renesting also may increase adult mortality during the season. Each failed nest represents an increase in the total investment of a parent in reared offspring during a single season. Mallard hens rely extensively on lipid reserves for the first, largest clutch, but with each renest dependence on environmental sources of nutrients increases as lipid reserves are depleted (Krapu 1981, Gatti 1983). Although it has never been measured, nutrient depletion probably increases adult mortality in Mallards as it does in geese (Ankney and MacInnes 1978).

In addition to energetic costs, renesting incurs increased predation risk for the hen. Red fox predation is a major cause of hen mortality during the breeding season (Johnson and Sargeant 1977, Sargeant et al. 1984). Even if the probability of predation remains constant during the season (Klett and Johnson 1982), a renesting hen is more likely to be killed than one that nests only once.

Our interpretation of clutch-size decline is similar to that proposed by Toft et al. (1984) in that both involve seasonal change in the probabilities of survival. Our results agree that Mallard clutch-size decline is due entirely to renesting. Mallards are an exception to Toft et al.'s hypothesis that clutch-size decline reflects equal alternative strategies of first nesters, and that assumes a seasonal decrease in mortality of very young broods. Unlike their prediction, we found no relationship between initiation date and the size of the first clutch. Our interpretation of clutch-size decline and egg-size increase with time of season depends, in part, on an assumed increase in mortality of very young ducklings as the season progresses. The life-history strategy in Mallards may involve a flexible response to unpredictable pond availability caused by a highly variable prairie environment and forced renesting in an environment of predictable habitat deterioration during the season.

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