ants. While it was not possible to test this directly, data were gathered as to the absolute abundance of *Melinaea* and *Mechanitis* in the presence and in the absence of ant swarms (13). Table 2 shows that capture of new female individuals per hour is significantly higher at swarms, roughly ten times the capture rate in the absence of a swarm, suggesting that the butterflies are strongly attracted to the swarm area or remain in the area once encountered, or both. Since females lack scent scales, the predominantly female concentrations probably are not self-aggregating as are the courtship groups. The butterflies may be using the strong odors produced by *E. burchelli* swarms for orientation to the swarm area, although once in the swarm vicinity, other factors, such as visual cues, are important in locating bird droppings.

We observed the behavior of the butterflies briefly before capturing them. At ant swarms, 49 percent of the butterflies captured were involved in feeding behavior; 26 percent were actually feeding on bird droppings, while the other 23 percent were flying low over the ground and stopping to examine white spots, such as lichens or fungal mycelium, which resemble bird droppings. Of the remaining 51 percent, 37 percent were flying, 7 percent were sitting on leaves, and 7 percent were alternating between flying and sitting. Some of these 51 percent may also have been involved in feeding behavior at the swarm, although this was not observed in the brief interval before capture.

Ithomiine butterflies are well-known aposematic models for mimicry complexes (14) and are not attacked by the insectivorous birds present at the swarms. Bird droppings at ant swarms could be a resource available only (i) to those butterflies and other large insects that are protected from bird predation by distasteful compounds or (ii) to palatable Batesian mimics of such species.

Drummond (15) first reported the association between butterflies and army ants. He observed females of *Mechanitis lysimnia doryssus* and *M. polymnia isthmia* (16) following a swarm of *E. burchelli* in Honduras. Drummond hypothesized that the *Mechanitis* were attracted to the swarm by an odor that mimicked the courtship scent of the male butterflies, thus explaining why only females were attracted to the swarm. Since Drummond made this hypothesis, it has been shown that *Mechanitis* males as well as females are attracted to the courtship scent (12); thus his hypothesis does not explain why predominantly females are found at the ant swarms. While Drummond observed the same dipping flight pattern that we observed, he did not see them alighting to feed on bird droppings.

Young (9), who did not observe the phenomena, responded to Drummond by suggesting the alternative hypothesis that "butterflies were being 'fooled' by the swarm raid odors. The odors of decay associated with the swarm raid triggered food searching behavior by these butterflies, causing them to follow the army ants." Our observations suggest that the butterflies are not being fooled at all, but rather take advantage of the swarm as a predictable source of an important nutrient.

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Evolution of Clutch Size in Birds: Adaptive Variation in Relation to Territory Quality

Abstract. *Reproductive output from enlarged or reduced magpie broods showed that each female generally lays a clutch of optimal size. This size varies considerably between females. Approximately 85 percent of the within-years variation in clutch size was associated with differences between territories. Colonial bird species, lacking individual foraging territories, have a smaller clutch size variation than territorial species.*

Lack (1) postulated that clutch size in birds is adjusted to the maximum number of nestlings for which the parents can find food. Provided that clutch size is largely inherited (2), the most productive clutch size will, by the force of natural selection, be the commonest one (1). Here I further develop this hypothesis, and propose that in a bird population there is not only one optimal clutch size but many. The optimal strategy for the birds is to be highly flexible in their choice of clutch size, in order to adapt clutch size to available resources. Territory quality is the most important factor in determining the optimum clutch size in territorial birds.

To support this hypothesis I present experimental field data from a breeding population of magpie *Pica pica*, showing that the optimal clutch size is *n* for birds that choose to lay *n* eggs, regardless of the actual value of *n*. Clutch size variation between different birds in the same territory and the same birds in different territories indicates that 81 to 86 percent of the within-years variation in magpie clutch size is linked to differences in territories. Furthermore, the influence of exclusive foraging areas on clutch size variation is reduced in birds breeding in colonies, and this leads to a smaller clutch size variation in colonial than in territorial species.

To analyze optimal clutch sizes in a population of individually marked mag-

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pies in south Sweden, I enlarged or reduced broods of various sizes by adding or removing nestlings in three breeding seasons. Reproductive output of different clutch and brood sizes, and mean nestling weights, are shown in Table 1. Comparison of unmanipulated clutches of different sizes indicates that birds which lay many eggs have the highest reproductive output. This has been found also in other species (*3*), and seems to be in conflict with Lack's original hypothesis (*4*). It has been suggested that a high adult mortality due to increased breeding effort in pairs with large clutches may explain this discrepancy between observations and Lack's hypothesis (*5*). However, I have demonstrated that adult survival in the magpie is positively correlated with clutch and brood size, a result that I have interpreted as an effect of differential territory quality, a high territory quality being associated with a large clutch size as well as with a high adult survival rate, and vice versa (*6*). Hence, I suggest that the average clutch size is optimal, not to all birds in the population, as stated by Lack (*1*), but only to birds with average territory quality. The optimal strategy therefore, for birds with territories of high quality is to lay large clutches, and for birds with poor territories to lay small clutches. Natural selection to a large extent operates on the ability of the birds to acquire a high-quality territory, permitting a large clutch size and a high reproductive success.

My experiments with manipulated brood sizes show that clutch sizes originally chosen by the birds are optimal. Comparison of reproductive output from all normal (n) broods with ($n - 2$), ($n + 1$), and ($n + 2$) broods reveals significant differences at $P < .05$, .02, and .01, respectively (Mann-Whitney U test; two-tailed). Predation affected n broods (24 percent predation) significantly less than ($n + 1$) broods (64 percent; $P < .03$, Fisher exact probability test) and ($n + 2$) broods (67 percent; $P < .04$). The number of fledglings in nests not preyed upon was significantly larger in n broods (2, 2, 3, 3, 4, 4, 4, 4, 4, 5, 5, 5, 7; 58 percent success) than in ($n + 2$) broods (1, 1, 2, 3; 26 percent success) ($P < .01$, Mann-Whitney U test), with ($n + 1$) broods (2, 2, 4, 4, 6; 49 percent success) falling in between these extremes. This reflects a higher rate of starvation in enlarged broods as compared to normal ones ($P = .02$; Mann-Whitney U test). Average nestling weight just before nest leaving (Table 1) varied only slightly, and therefore postfledging mortality probably affected all clutch and brood sizes to a similar extent.

I also compared fledgling production of individually marked pairs, which in 1 year attended an enlarged brood and another year an unmanipulated one. One pair had a higher, four pairs had the same, and ten pairs had a lower fledgling production in the year of extraparental stress ($P < .025$; t-test, paired means).

Variation in clutch size in relation to female, territory, and year is shown in Table 2. Magpies usually forage within 100 m from their nest, and shifts of nest sites less than 200 m, leading to overlap between old and new territories, are not considered as changes in territory. If one mate dies, the territory is usually taken over by a new pair. Therefore, variances A, C, and D in Table 2 may contain certain fractions of variation that are linked with differences between males. Provisionally, I assume the variance caused by differences between males to be negligible, but this is not a critical assumption for the results described below.

Ideally, the variances in Table 2 should satisfy the condition $A = C + D - 2B$, and, indeed, this is satisfactorily fulfilled ($A = 0.70$ and $C + D - 2B = 0.67$). As clearly seen from Table 2, a major part of the clutch size variation is caused by differences in territories. The proportion of total within-year variance linked with differences in territories is $(D - B)/$

Table 1. Reproductive output (R.O.) in the magpie, in terms of average number of young immediately before nest-leaving, and mean of mean nestling weight (W) within brood at 22 to 28 days of age, in relation to clutch and brood size. Nestlings of 0 to 3 days of age were added or removed to attain various brood sizes in pairs with different clutch sizes. The procedure of nestling transfers lasted less than 1/2 hour, and hatching asynchrony was imitated in recipient broods, with transferred nestlings being among the first hatched young in donor broods. The number of clutches is given in parentheses.

Initial clutch size	Brood size, natural and manipulated										
	4		5		6		7		8		9
	R.O. (No.)	W (g)	R.O. (No.)	W (g)	R.O. (No.)	W (g)	R.O. (No.)	W (g)	R.O. (No.)	W (g)	R.O. (No.)
5	0.3 (3)	210 (1)	0.7 (3)	204 (1)	0.5 (4)	224 (1)	0.3 (4)	163 (1)	0 (3)		
6	1.7 (7)	197 (3)	1.9 (7)	200 (4)	2.8 (5)	204 (4)	0.8 (5)	193 (1)	1.2 (5)	191 (3)	
7	3.5 (2)	227 (2)	2.3 (9)	208 (7)	3.1 (7)	202 (5)	3.6 (5)	200 (4)	2.4 (5)	191 (3)	0 (3)
8	2.5 (2)	208 (2)	3.5 (4)	211 (2)	3.5 (2)	207 (2)	4.3 (4)	200 (4)	4.5 (4)	203 (4)	

Table 2. Variances (± S.E.) of clutch size in a population of individually marked magpies from 1973 to 1979. Variances were calculated on the basis of all available pair combinations of clutch size values. In this way, selectively large weight is given to females and territories with long series of clutch sizes (*2*). However, almost identical results are found if all females and territories are given equal weight. The variance in set A is the mean of 3 years. The variance in set B is based on data for 25 females and territories, in set C on 32 shifts of females in given territories, and in set D on 11 shifts of territories by females.

Set	Between	Within	Variance
A	Females and territories	Years	0.70 ± 0.03
B	Years	Females and territories	0.27 ± 0.06
C	Females and years	Territories	0.37 ± 0.06
D	Territories and years	Females	0.84 ± 0.17

Table 3. Coefficient of variation (C.V.) of clutch size in colonial and territorial birds. Calculations were made from the references given. Where different breeding pairs use more or less common foraging areas birds are regarded as colonial, and those with largely exclusive foraging areas are regarded as territorial.

Colonial birds				Territorial birds			
Species	C.V.	n	Reference	Species	C.V.	n	Reference
Podiceps nigricollis	21.5	219	(*7*)	*Podiceps auritus*	27.2	354	(*8*)
Egretta garzetta	13.7	60	(*9*)	*Ixobrychus minutus**	20.2	92	(*9*)
Falco vespertinus	15.3	59	(*10*)	*Falco subbuteo**	29.3	22	(*10*)
Riparia riparia	11.2	49	(*11*)	*Hirundo rustica*	14.9	115	(*12*)
Turdus pilaris†	10.6	163	(*13*)	*Turdus merula*†	17.3	33	(*14*)
Corvus frugilegus	18.7	137	(*15*)	*Corvus corone*	23.1	120	(*17*)
Corvus monedula	23.8	27	(*16*)	*Corvus monedula*	26.0	22	‡
Sturnus vulgaris	12.6	22	(*18*)	*Sturnus vulgaris*	17.4	27	(*18*)

*Several years. †First clutches. ‡Own observations.

$A = 81$ percent or $(A + B - C)/A = 86$ percent. The remaining part of the within-year variance, 19 or 14 percent, is due to differences between individual females. These differences between females may be hereditary, but may also be due to other factors, like differences in feeding efficiency.

If territory quality is an important factor in determining optimum clutch size, one should expect a generally smaller clutch size variation in colonial species, without exclusive foraging areas in the different breeding pairs, than in territorial species. Coefficients of variation of clutch size in species being both colonial and territorial, and of ecologically similar species, belonging to one of the two categories (Table 3), fit this prediction.

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Correction of Enzyme Deficiency in Mice by Allogeneic Bone Marrow Transplantation with Total Lymphoid Irradiation

Abstract. *Enzyme deficiency was corrected in mice after allogeneic bone marrow transplantation without occurrence of graft versus host disease. β-Glucuronidase-deficient C3H/HeJ mice were treated with total lymphoid irradiation. Normal bone marrow cells (30×10^6) from BALB/c mice were infused 1 day after total lymphoid irradiation, with resulting stable BALB/c to C3H/HeJ chimeras (> 90 percent circulating donor-type cells) without graft versus host disease. β-Glucuronidase activity increased to normal levels in all chimeras as measured in the liver and in the plasma. Activity was maintained throughout an observation period of 7 months.*

Enzyme replacement therapy is the most desirable and the only rational goal for correction of the many varieties of enzyme deficiency disorders in man. There has been only limited success for enzyme replacement strategies that involve directly administered purified enzymes, enzyme-rich plasma, or placental fractions (*1-5*), enzyme-containing semipermeable microcapsules (*6*), erythrocyte and liposome-entrapped enzymes (*7-10*), and enzyme preparations attached to physiological carrier molecules (*11, 12*). The usefulness of some of these approaches has been limited by relatively short-circulating and intracellular half-life, susceptibility to various degradation processes—predominantly by the reactivity of the immune system against the foreign proteins—and the limited distribution into various cellular compartments. Enzyme-producing allogeneic cells or whole organs may provide a better potential intrinsic physiological source of deficient enzymes.

Whole organ (kidney, liver, and pancreas) and cellular (fibroblasts and bone marrow) transplantations have already been attempted experimentally for the treatment of enzymatic and metabolic disorders (*13-19*). Initial results were encouraging, but the long-term success of organ transplantation has been rather limited, mostly as a result of unsolved problems in overcoming rejection (*20-27*). We have explored the feasibility of enzyme reconstitution in deficient mice by evaluating the effectiveness of continuous enzyme supply by allogeneic bone marrow cells. The attempt to use allogeneic bone marrow transplantation for the reconstitution of enzyme-deficient recipients imposes obstacles, including the so-called double barrier of host versus graft (HVG) and graft versus host disease (GVHD). We now report a new approach to enzyme replacement therapy by allogeneic, strongly histoincompatible bone marrow grafts obtained from normal enzyme-producing donors after enzyme-deficient recipients were treated with total lymphoid irradiation to ensure engraftment and prevent GVHD. The preparation of recipients with a single high-dose whole-body irradiation or with a high dose of cyclophosphamide instead of total lymphoid irradiation resulted in a vigorous lethal GVHD after bone marrow transplantation.

Total lymphoid irradiation, a relatively safe form of radiotherapy originally used for the treatment of human malignant lymphomas (*28*), was developed in the last few years as a new regimen to condition recipients of subsequent bone marrow and organ allografts (*29-35*). Permanent and stable bone marrow allo-

Table 1. Hydrolase activities in the liver and plasma of untreated C3H/HeJ, normal BALB/c mice, and BALB/c → C3H/HeJ chimeras 50 days after total lymphoid irradiation and marrow transplantation. C3H/HeJ mice were treated with daily doses of 200 rads (for 17 days) to expose the major lymphoid organs, including the thymus and spleen [as described in (*29, 30*)]. One day after completion of irradiation, 30×10^6 BALB/c bone marrow cells were infused. Individual samples of heparinized blood and liver biopsies were obtained from untreated C3H/HeJ ($N = 20$), BALB/c ($N = 17$), and BALB/c → C3H/HeJ chimeras ($N = 6$) 50 days after bone marrow transplantation. Hydrolase activities of β-glucuronidase and two unrelated enzymes (β-galactosidase and *N*-acetyl-β-glucosaminidase) were assayed simultaneously in the plasma and in the liver homogenate (*37*). Data are expressed as means ± standard deviations (S.D.).

	C3H/HeJ		BALB/c		BALB/c → C3H/HeJ chimeras	
	Liver*	Plasma†	Liver	Plasma	Liver	Plasma
β-Glucuronidase	23.4 ± 7.0	9.5 ± 2.0	135.0 ± 30.2	20.4 ± 4.6	207.8 ± 82.2	16.5 ± 5.0
β-Galactosidase	146.9 ± 50.0	34.7 ± 13.2	137.0 ± 27.0	34.4 ± 27.0	155.3 ± 62.3	22.0 ± 4.3
N-Acetyl-β-glucosaminidase	1257.2 ± 476.0	1151.3 ± 204.6	1082.1 ± 224.6	854.6 ± 177.6	1320.6 ± 411.1	975.0 ± 261.9

*Specific activity is expressed as nanomoles per hour per milligram of protein. †Specific activity is expressed as nanomoles per hour per milliliter of plasma.