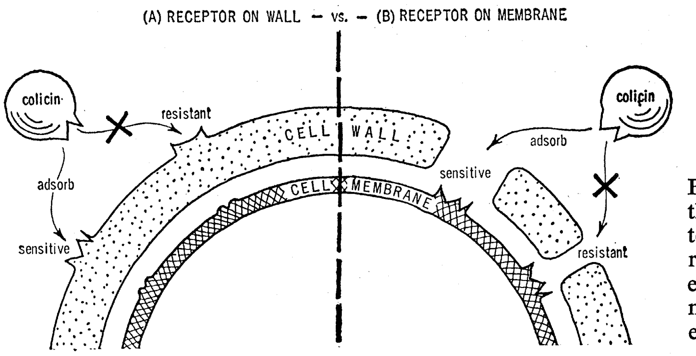

Fig. 3. Models for the colicin E1 receptor and the nature of resistant mutants. The experiments support model B against model A.

remains as free proline or whether it is incorporated into proteins. Kaback and Stadtman (*5*) showed that more than 80 percent of the ^{14}C accumulated by the membrane vesicles could be extracted in a form chromatographically identical with free [^{14}C]proline. In our control experiments more than 85 percent of the [^{14}C]proline accumulated by the membranes remains soluble in cold trichloroacetic acid.

We conclude from the sensitivity of proline transport in subcellular membrane vesicles to colicin E1 that the receptor sites for the colicin are on the cell membrane (Fig. 3B) and not on the cell wall (Fig. 3A). The previously standard model (*1*) for the receptor on the wall (Fig. 3A) is based on the existence of the class of mutants that are resistant to the otherwise unrelated colicins E1, E2, and E3 and to bacteriophage BF23. However, if the phage receptor on the cell wall includes the molecular configuration which we have diagrammatically represented as a wide or narrow channel in Fig. 3B, this would account for the experimental fact that resistant mutants adsorb neither the phage nor the colicins. In our model, the resistance of the resistant mutant to colicin E1 is not due to a change in the shape of the receptor (Fig. 3A) but due to a change in the cell wall which blocks access to the membrane receptor (Fig. 3B). When the wall is enzymatically removed, as in the preparation of membrane vesicles, then the colicin E1 receptor is again accessible. Variations on the model in Fig. 3B are readily devised, but this model has the virtue of predicting the existence of still additional classes of mutants with altered sensitivity and adsorption properties. Some may have already been found by Hill and Holland (*4*), and one specific class which is predicted by the model would be resistant and unable to adsorb colicin E1 owing to a change in the membrane receptor (which would still be present on the isolated membranes). The characterization of other classes of colicin-resistant and tolerant mutants through studies of isolated membranes and the physical isolation of the product of the *tol C* gene from the membranes are reasonable goals.

PINAKILAL BHATTACHARYYA
LOUIS WENDT
ELEANOR WHITNEY
SIMON SILVER
Department of Biology, Washington University, St. Louis, Missouri 63130

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8. Supported by NIH grants AI 08062 and FR 6115. L.W. was supported in part by NIH training grant 5 T1 GM 00714. J. P. Kabat (in S. E. Luria's laboratory) has also found that colicins E1 and K affect proline transport by vesicles (personal communication) and is studying vesicles from other classes of tolerant mutants.

5 January 1970; revised 17 February 1970 ■

Nest Parasitism, Productivity, and Clutch Size in Purple Martins

Abstract. *Mean maximum nestling weight of purple martins decreased with increase in brood size from three to five. Martins in the absence of acarine nest parasites produced young heavier than parasitized young of the same brood size; in addition, unparasitized nestlings tended to reach a maximum weight equivalent to that of young in parasitized broods of one less member. Modal brood size for parasitized and unparasitized martins was four, but there was a significant trend toward production of broods of five by mite-free birds, and of broods of three by parasitized parents. This suggests a potentially important role for nest parasitism in the determination of clutch size in martins and other birds.*

Analysis of data from two colonies of the purple martin, *Progne subis* L., has demonstrated a significant decrease in productivity that accompanies nest parasitism by blood-feeding mites (*1*). The evidence indicates that nest parasitism may be important in natural selection of avian clutch size, although this possibility has been largely ignored in discussions of clutch size (*2*).

Two martin colonies were established in the spring of 1964 in Lawrence, Kansas, and are still being maintained. Situated 10 m apart, each colony consists of 12 apartments constructed to allow daily examination of contents and removal of nestlings for weighing and other purposes. Shortly after establishment, both colonies became infested with mites, chiefly the martin mite, *Dermanyssus prognephilus* Ewing (*3*). Dipterans, reportedly significant nest parasites of martins (*4*), did not appear in our colonies.

Martin mites taken from the colonies were maintained in laboratory culture (*5*), with the domestic fowl as host. Two-week-old chicks introduced as hosts generally died within a relatively short time, frequently in as little as 3 hours. Cause of death is not yet known, but it seems more likely to be due to toxicity of the mite saliva than to exsanguination by the mites in so short a time. Co-evolution of host and parasite over a period of time has been shown to result in a reduction of the harmful effects of the parasite on its host (*6*), and it is possible that the scarcity of studies of the effect of nest parasitism on productivity of avian hosts may be due to an assumption that such a relation would be difficult to demonstrate as a result of long-term, mutual evolution. Our observation of the extremely severe effects of *D. prognephilus* on the domestic fowl, an abnormal host, suggested that these mites were likely to produce a lesser, but nevertheless measurable, effect on the productivity of their natural host, the purple martin (*7*).

To test this hypothesis, one of the martin colonies was treated each year during the nesting season with a mixture of the acaricidal dusts, Dri-Die 67 and Dibrom (*8*). Mites were never completely eradicated from the treated martin colony, but a majority of mites was destroyed, which created a highly significant population differential between the two colonies. Occasional seasonal alternation of treatment from one colony to the other provided no evidence for the preferential choice of a mite-free colony by birds returning in the spring. Presumably, small populations of overwintering mites tend to make the colonies equivalent in their attractiveness to returning martins.

Daily weights of nestlings in the two colonies were good indicators of parasite influence. Nestlings (Fig. 1, A and B) show an early, rapid growth phase which declines slightly in rate with age, reaching a peak and then dropping off as the nestlings lose weight and prepare for flight (*9*).

Martin productivity is influenced by a complex of interrelated and interacting factors, including weather conditions, availability of food and nest sites, presence of nest-site competitors and predators, age of parents, seasonal timing of nesting, and nest parasitism (*1*). In the generally favorable season of 1966 (warm, dry, sunny weather), the weight curves of parasitized and unparasitized young are essentially identical throughout their period of rapid and slow growth, but separate after reaching a maximum, with parasitized young losing weight more rapidly, and fledging lighter ($P < .001$) than unparasitized young (Fig. 1B and Table 1). In contrast, in the less favorable 1967 season (characterized by heavy rains and cooler temperatures), parasitized young were lighter than their unparasitized counterparts throughout almost the entire period in the nest. In 1965, a warm, wet nesting season led to extremely large mite populations in the untreated colony. Although initial occupancy was the same and an equivalent number of eggs was produced in both colonies in 1965, nearly all nest boxes and eggs were deserted by martins in the untreated colony, apparenty to escape the large numbers of parasites. Similar nest desertions accompanying large populations of the mite *Ornithonyssus sylviarum* (Canestrini and Fanzago) have been noted for mynahs and starlings (*10*), and infestations of the same mite cause significant mortality in phoebes by driving young from the nest prematurely (*11*).

Table 1. Mean daily weights and percent difference between daily weights of purple martin nestlings from treated and untreated colonies in the 1966 season. With the paired comparisons test, $t = 4.322$, for 28 d.f. ($P < .001$).

Day	Mean daily weight (g)		Percent difference
	Treated	Untreated	
1	3.72	3.67	1.36
2	5.45	5.31	2.64
3	8.09	7.97	1.50
4	11.63	11.52	0.95
5	15.91	15.69	1.40
6	20.47	20.11	1.79
7	25.32	25.09	0.92
8	30.67	30.38	0.95
9	35.69	35.48	0.59
10	40.34	40.38	−0.01
11	43.99	44.17	−0.41
12	47.35	48.01	−1.39
13	51.02	51.04	−0.00
14	52.77	53.34	−1.08
15	54.31	53.99	0.59
16	54.49	54.64	−0.28
17	55.04	54.63	0.75
18	54.97	53.33	3.08
19	55.71	52.37	6.38
20	55.24	51.63	6.99
21	54.23	50.89	6.56
22	53.20	49.85	6.72
23	52.68	49.26	6.94
24	51.67	48.08	7.47
25	51.05	48.09	6.16
26	48.93	47.37	3.29
27	48.74	46.35	5.16
28	48.12	46.32	3.89
29	47.52	44.85	5.95

With few exceptions, mean maximum nestling weight tends to decrease with increase in brood size from three to five (Table 2). However, the influence of availability of resources and parasitism appears less pronounced at lower brood sizes (*12*). A plot of mean maximum weight attained by nestlings in the two houses in 1966, for which we have the best replication (Fig. 2), shows an expected decline in weight with increased brood size. In addition, the maximum weight of parasitized nestlings in 1966 was roughly 7 percent lower than that of parasite-free nestlings of the same brood size. Further, maximum weights attained by parasitized young reared in broods of four and three did not differ statistically from maximum weights of unparasitized nestlings in broods of five and four, respectively; that is, there was a tendency for parent birds in the mite-free colony to rear one more offspring than parents in the parasitized colony, with no sacrifice in the weight of the young (*13*) (Fig. 2).

A positive relation between maximum nestling weight and survival after fledging seems likely in purple martins, although our banding returns are meager. However, a high correlation

Table 2. Mean maximum weight attained by purple martin nestlings of different brood sizes reared in the presence (U) and absence (T) of nest parasites during the 1965–1969 seasons. Numbers in parentheses represent *n* and standard deviation for each measurement. A single asterisk between two measurements indicates significance at $P < .05$, and triple asterisks indicate significance at $P < .001$ (*t*-test).

Year	Parasite condition	Mean maximum weight of nestlings (g) in broods of:			
		Three	Four		Five
1965	T		62.84 (8;2.909)	***	56.30 (10;1.230)
	U	60.23 (3;3.118)			
1966	T	61.81 (3;3.385)	58.95 (12;3.475)	*	56.09 (20;3.399)
			*		*
	U	57.60 (12;5.688)	55.26 (20;4.395)		52.62 (5;2.006)
1967	T	59.27 (3;0.602)	57.29 (8;1.632)	*	50.48 (5;4.219)
			***		
	U		54.38 (8;0.937)		
1968	T		60.36 (12;1.816)		
			***		
	U	55.90 (6;2.825)	56.09 (8;2.181)	*	59.72 (5;3.562)
1969	T	57.93 (3;1.553)	62.45 (4;2.921)		56.52 (5;4.327)
		*	*		
	U	60.37 (6;0.728)	56.39 (8;4.679)		

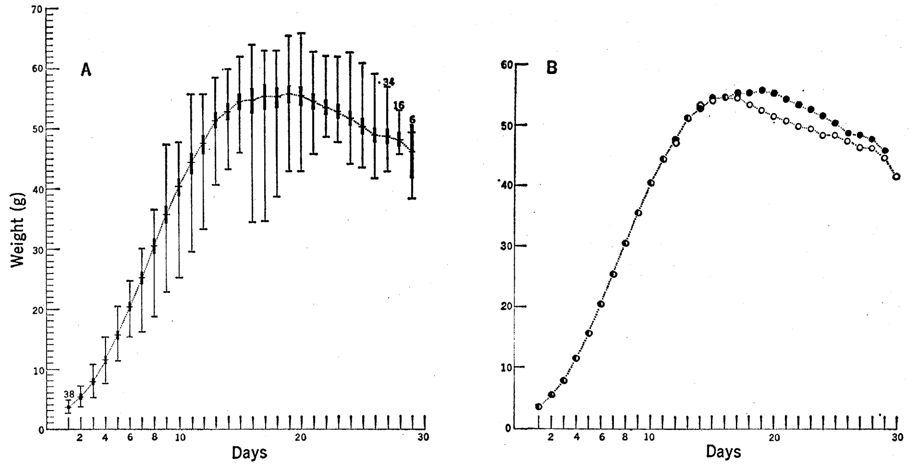

Fig. 1. Nestling weights of purple martins, 1966 season, reared in the absence of nest parasites (A), and mean weights in both absence (solid circles) and presence (open circles) of parasites (B). Sample size for treated replicates in (A) and (B) is 38, unless otherwise noted. The horizontal bars represent maximum, mean, and minimum; the solid rectangles represent the 95 percent confidence limits. Sample size for untreated replicates in (B) is 39 for days 1–22, 37 for day 23, 35 for day 24, 29 for day 25, 24 for day 26, 19 for day 27, 12 for day 28, 2 for day 29, and 1 for day 30. Mean brood size was 4.2 for the treated colony and 3.5 for the untreated.

between fledging weight and subsequent survival has been found in other birds (*14*) and, in our study, the few fledglings that we have found on the ground and too weak to fly have all come from the untreated colony. As mean maximum nestling weight declines with increasing brood size (Fig. 2), we can assume the existence of a brood size at which probability of fledgling survival approaches or becomes zero. Accordingly, natural selection for an otherwise advantageous increase in clutch size (and, therefore, brood size) would be counterbalanced by the decreased capability of lighter weight fledglings from large broods to survive. Our data indicate that selection for smaller clutch size will be accentuated by the presence of nest parasites. Feeding activities of the latter tend to further depress nestling weight and, therefore, should mitigate against the eventual survival of parasitized young to reproductive age.

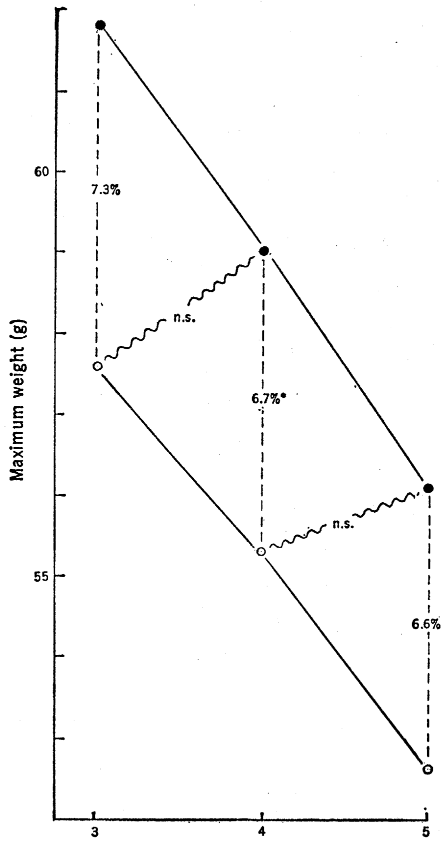

Fig. 2. Mean maximum weight attained by individuals of different brood sizes reared in the presence (open circles) and absence (solid circles) of nest parasites, 1966 nesting season. Asterisk indicates significance by *t*-test at $P < .05$. The difference of 7.3 percent for brood size of three, although probably indicative of a real trend, is not statistically significant because of small sample size from the treated colony.

Further evidence for such selection can be seen by summarizing martin productivity in terms of the number of broods of different sizes (three to five) produced in the presence and absence of parasites. Over the 6 years, 24 pairs of martins from the treated colony and 25 from the untreated fledged 15 broods of three (4 broods from the treated : 11 from the untreated), 24 broods of four (12 : 12), and 10 broods of five (8 : 2). Thus, although modal brood size of both mite-free and parasitized parents was equal, a shift occurred in the direction of larger broods in the absence of parasites and smaller broods in their presence ($P < .05$ by χ^2 test, with Fisher's Exact Method), with a mean of 4.2 young produced by mite-free birds versus 3.6 young by parasitized martins.

Avian clutch size is an easily measured variable thought to relate to resource availability and to basic differences between temperate and tropical ecosystems. Historically, the evolution of clutch size has been regarded primarily as a function of the amount of food that the parent birds are able to provide or the incidence of nest predation, or both, with the potential role of nest parasitism either being ignored or being considered minimum. The incidence and degree of nest parasitism may be a significant limiting factor in the evolution of clutch size in the purple martin and, by extension, in other cavity-nesting birds which return to the same nest sites year after year.

W. WAYNE MOSS*
Division of Entomology,
University of California,
Berkeley 94720

JOSEPH H. CAMIN
Department of Entomology,
University of Kansas, Lawrence 66044

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7. It also seems reasonable to assume that such an effect might be somewhat accentuated by the relatively recent appearance of man-made, multiple-unit martin houses, which have resulted in higher martin nesting densities than were usual for tree-hole nesting martins before the arrival of European man in North America.
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Phila. Herpetol. Soc. **9**, 11 (1961); *Calif. Agric.* **15**, 8 (1961); *Angew. Parasitol.* **8**, 210 (1967); J. H. Camin, G. K. Clarke, L. H. Goodson, H. R. Shuyler, *Zoologica* **49**, 65 (1964). Dri-Die 67 is a finely divided silica aerogel, containing 4 percent ammonium fluorosilicate. It is not toxic to ectoparasitic arthropods, but it abrades the epicuticle and adsorbs the cuticular lipids, destroying the waterproofing properties of the cuticle and causing death from desiccation. Dibrom, $C_4H_7Br_2Cl_2O_4P$, is an aliphatic derivative of a phosphorus compound and is toxic to the mites. The action of Dri-Die 67 apparently aids the penetration of Dibrom and enhances the toxicity of the latter. Neither acaricide is toxic to the bird hosts.

9. R. E. Ricklefs [*Auk* **85**, 30 (1968)] has analyzed weight recession in the barn swallow and elsewhere [R. E. Ricklefs, thesis, University of Pennsylvania (1967)] has derived equations describing the growth curves of martins and other birds.
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12. Mean maximum nestling weight (MMW; Table 2) was greater for broods of three than for broods of four nestlings in four of six available comparisons. In one case (1968, untreated) the weights were approximately equal, and in another (1969, treated) the MMW of a single brood of four was greater than that of a single brood of three nestlings. In no case, however, was the difference significant. On the other hand, in five of six available comparisons the MMW was greater for broods of four than for broods of five nestlings, and in three cases these differences were significant. The single case in which the MMW was greater for a brood of five than for four nestlings was also significant, but this case (1968, untreated) involved only one brood of five nestlings, and the unexpectedly high weights of these birds may be attributable to unusual food-gathering proficiency of a single pair of parents. In seven available comparisons of treated versus untreated broods of equivalent sizes, the MMW was greater for the treated than for the untreated birds in six cases, and in five of the six cases the differences were statistically significant. In only one instance (1969) was the MMW greater for the untreated broods and in this case the brood size was three, the lower end of the range, at which the food-gathering ability of the parents may be able to compensate for the drain of parasitism.
13. Although several days may elapse between laying of the first and last eggs of a clutch, all nestlings in a given nest tend to hatch on the same day. Weights of nestlings within one brood did not differ significantly over the season when tested according to order of hatching, which indicates that parents tended to distribute the available food more or less evenly among their young. The trend toward equivalent MMW for broods of n in the untreated colony and $n+1$ in the treated colony was contradicted in the one case where a comparison could be made for the 1967 season (U-4 vs. T-5, Table 2) but was confirmed for the 1965 season (T-4 vs. U-3), the 1968 season (T-4 vs. U-3), and the 1969 season (T-4 vs. U-3; T-5 vs. U-4).
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* On leave from the Academy of Natural Sciences, Philadelphia, Pa. 19103 and the Department of Biology, University of Pennsylvania, Philadelphia.

15 December 1969; revised 3 March 1970

Formation Flight of Birds

Abstract. *Formation flight of birds improves aerodynamic efficiency. Theoretically, 25 birds could have a range increase of about 70 percent as compared with a lone bird, the advantage being more pronounced when there is a tail wind. A vee formation is required to equally distribute the drag saving, and, contrary to other statements, the lead bird does not necessarily have the most strenuous position. The angle of the predicted vee compares with that observed in nature; stability mechanisms are described which make it easy and natural for the bird to sense optimal formations.*

Many birds migrate over long distances, some adopting a very specific vee formation in flight. Aerodynamicists have speculated that this formation is chosen to reduce flight power demand.

Wieselsberger (*1*) suggests that a vee formation would be desirable for approximate equipartition of drag. Because of the simplified analysis only small power savings were indicated. Others, for example, Storer (*2*), describe the mechanism of drag reduction by formation flight without quantitative analysis. There are certainly small power savings for some formations of aircraft, but this reduction occurs only for a dangerously close formation. We have completed a theoretical analysis of formation flight of birds, considering the greater aerodynamic freedom of animal flight. Our results showed that a striking saving in power occurred. Typically, a group of 25 birds has approximately 71 percent more range than a lone bird, and the vee formation is optimal, with the angle predicted consistent with observations. Also, the aerodynamics of optimal formation flight introduce certain invariants which can readily be sensed, making it easy and natural for the bird to fly optimally.

We first established the fixed-wing analog. By applying standard, unsteady wing theory to the ornithopter problem we showed that the flapping power required consists of three terms. Two of these, the profile power and the induced power, are of the same size. The third term, representing flapping losses, is of low magnitude if the ratio of the tip flapping speed to the flight speed is low. The profile power and induced power are identical to those required if the wing were fixed and propelled by other means. Thus, analyzing the bird as a fixed-wing aircraft gives a good estimate of its cruise power requirements. So we considered a fixed-wing vehicle of the same geometry as the bird.

It is a basic principle of aerodynamics that an object flying by dynamic lift in a fluid gets its lift by creating downward momentum within its span. This applies to fish or fowl, airplane or submarine. Beyond the wing there is an upwash field, which is very intense near the tip. Figure 1 shows streamlines and vertical velocities of this flow field. The power needed to generate this lifting momentum is called induced power, which is distinguished from the profile power—the power needed to drive the vehicle through the fluid against skin friction. There is an infinite number of downwash distributions for a given lift. For example, for increased tip lift the downwash at the tip will be stronger than that inboard on the wing. Induced power depends critically on downwash distribution, which itself is related to the distribution of lift across the wing (the spanwise loading). A theorem of

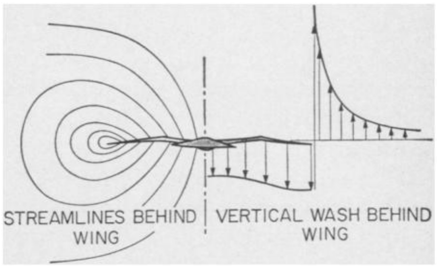

Fig. 1. Flow field of lifting wing.

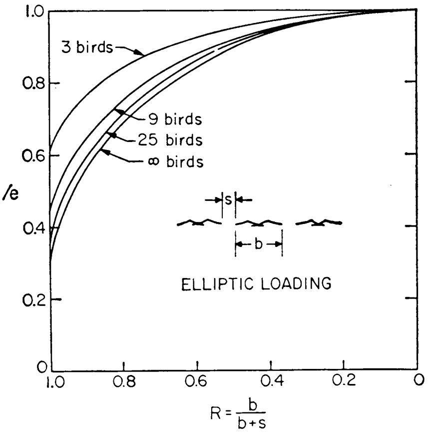

Fig. 2. Drag saving by formation flight.