Mediterranean avian seed dispersers. Ecology 65: 609–617.

HOLTHUIJZEN, A. M. A., AND C. S. ADKISSON. 1984. Passage rate, energetics, and utilization efficiency of the Cedar Waxwing. Wilson Bull. 96:680–684.

HONIGMANN, H. 1936. Studies on nutrition of mammals, part 1. Proc. Zool. Soc. Lond. 1936:517–530.

JORDANO, P. 1987. Frugivory, external morphology and digestive system in mediterranean sylviid warblers *Sylvia* spp. Ibis 129:175–189.

KARASOV, W. H., E. PETROSSIAN, L. ROSENBERG, AND J. M. DIAMOND. 1986. How do food passage rate and assimilation differ between herbivorous lizards and nonruminant mammals? J. Comp. Physiol. B Comp. Biochem. 156:599–609.

LAUGKSCH, R. C., AND D. C. DUFFY. 1986. Food transit rates in Cape Gannets and Jackass Penguins. Condor 88:117–119.

LEVEY, D. J., AND W. H. KARASOV. 1989. Digestive responses of temperate birds switched to fruit or insect diets. Auk 106:675–686.

MALONE, C. R. 1965. Dispersal of plankton: Rate of food passage in Mallard ducks. J. Wildl. Manage. 29:529–533.

MITCHELL, P. C. 1901. On the intestinal tract of birds. Trans. Linn. Soc. Lond., Zool. 8:173–275.

NAIK, D. R. 1962. A study of the intestinal ceca of some Indian birds. M.Sc. thesis, Banaras Hindu Univ., Varanasi, Uttar Pradesh, India (copy deposited in Section of Birds Library, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania).

PROCTOR, V. W. 1968. Long-distance dispersal of seeds by retention in digestive tract of birds. Science 160:321–322.

ROBY, D. D., K. L. BRINK, AND A. R. PLACE. 1989. Relative passage rates of lipid and aqueous digesta in the formation of stomach oils. Auk 106: 303–313.

SUTHERS, H. B. 1985. Ground-feeding migratory songbirds as cellular slime mold distribution vectors. Oecologia 65:526–530.

WALSBERG, G. E. 1975. Digestive adaptations of *Phainopepla nitens* associated with the eating of mistletoe berries. Condor 77:169–174.

WARNER, A. C. I. 1981. Rate of passage of digesta through the gut of mammals and birds. Nutr. Abstr. Rev. Ser. B 51:789–821.

WHITE, D. W., AND E. W. STILES. 1990. Co-occurrences of foods in stomachs and feces of fruit-eating birds. Condor 92:291–303.

WILLSON, M. F. 1989. Gut retention times of experimental pseudoseeds by Emus. Biotropica 21:210–213.

ZISWILER, V., AND D. FARNER. 1972. Digestion and the digestive system. Pages 343–430 *in* Avian biology, vol. II (D. S. Farner and J. R. King, Eds.). Academic Press, New York.

Received 2 October 1991, accepted 23 February 1992.

The Auk 109(4):936–937, 1992

The Insurance Hypothesis and the Theory of Clutch Size in Birds and in Invertebrates

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The theory of adaptive clutch sizes began with Lack's (1947) hypothesis, formulated for altricial birds, that selection maximizes the number of young produced per nest. In addition to stimulating a large and continuing amount of research on avian clutch sizes (e.g. Blackburn 1991, Rohwer 1991), these ideas have been successfully applied to invertebrate clutch sizes. This in itself has become a thriving research area (Godfray 1987). Regrettably, it seems that, although essentially the same, these research areas at times have become estranged (but see Godfray et al. 1991).

Power et al. (1989) offered the following explanation for European Starling (*Sturnus vulgaris*) clutch sizes smaller than would "normally" maximize fitness: conspecific brood parasitism (CBP; the adding of eggs to a clutch by conspecifics) can result in an overcrowded nest and a drastic reduction in fledgling success. As an insurance against the possibility of CBP, the starlings lay a smaller clutch, which on average is more productive than a "normal" clutch laid without anticipation of CBP. Rothstein (1990) reported the Power et al.'s hypothesis as novel, but in fact the idea is essentially the same as one developed originally for hymenopteran parasitoids by Parker and Courtney (1984). Superparasitism in parasitoids (van Alphen and Visser 1990), or more generally superoviposition (Godfray 1987) in invertebrates, is analogous to CBP in birds. Using an ESS model to consider the clutches sequentially laid on the same host by two conspecific parasitoids, Parker and Courtney showed that the clutch size produced by the first female should decrease as the probability of super oviposition increases. The prediction that the probability of superparasitism influences clutch size has

since been made by a number of studies (Parker and Begon 1986, Ives 1989, Strand and Godfray 1989, van Alphen and Visser 1990, Visser et al. 1992). The "insurance" hypothesis has also been applied to the sex ratio produced by the first parasitoid to lay eggs: the sex ratio should become more male biased as the probability of superoviposition increases (Wylie 1976, Werren 1980, Suzuki and Iwasa 1981). Unlike the starlings studied by Power et al., however, there is as yet no empirical evidence for these behaviors among parasitoids.

The idea that clutch-size decisions are affected by the probability of egg laying by conspecifics is thus not novel, at least not to invertebrates. I share the concern recently expressed by Lawton (1991) that ecology is now so "big" that unhealthy taxonomic divides have arisen within it. Despite these divisions, Lack's (avian) theory was borrowed by those working on parasitoids, I find it encouraging that it is perhaps now time for this loan to be repaid across the taxonomic abyss.

This work was supported by an N.E.R.C. (U.K.) postdoctoral research fellowship.

Literature Cited

Blackburn, T. M. 1991. The interspecific relationship between egg size and clutch size in wildfowl. Auk 108:209–211.

Godfray, H. C. J. 1987. The evolution of clutch size in invertebrates. Ox. Surv. Evol. Biol. 4:117–154.

Godfray, H. C. J., L. Partridge, and P. H. Harvey. 1991. Clutch size. Annu. Rev. Ecol. Syst. 22:409–429.

Ives, A. R. 1989. The optimal clutch size of insects when many females oviposit on a patch. Am. Nat. 133:671–687.

Lack, D. 1947. The significance of clutch size. Ibis 89:309–352.

Lawton, J. H. 1991. Warbling in different ways. Oikos 60:273–274.

Parker, G. A., and M. Begon. 1986. Optimal egg size and clutch size: Effects of environmental and maternal phenotype. Am. Nat. 128:573–592.

Parker, G. A., and S. P. Courtney. 1984. Models of clutch size in insect oviposition. Theor. Popul. Biol. 26:27–48.

Power, H. W., E. D. Kennedy, L. C. Romagnano, M. P. Lombardo, A. S. Hoffenburg, P. C. Stouffer, and T. R. McGuire. 1989. The parasitism insurance hypothesis: Why starlings leave space for parasitic eggs. Condor 91:753–765.

Rohwer, F. C. 1991. Response to T. M. Blackburn. Auk 108:211–213.

Rothstein, S. I. 1990. Brood parasitism and clutch size determination in birds. Trends Ecol. & Evol. 5:101–102.

Strand, M. R., and H. C. J. Godfray. 1989. Superparasitism and ovicide in parasitic Hymenoptera: A case study of the ectoparasitoid *Bracon hebetor*. Behav. Ecol. Sociobiol. 24:421–432.

Suzuki, Y., and Y. Iwasa. 1981. A sex ratio theory of gregarious parasitoids. Res. Popul. Ecol. (Kyoto) 22:366–382.

van Alphen, J. J. M., and M. E. Visser. 1990. Superparasitism as an adaptive strategy. Annu. Rev. Entomol. 35:59–79.

Visser, M. E., J. J. van Alphen, and L. Hemerik. 1992. Adaptive superparasitism and patch time allocation in solitary parasitoids: An ESS model. J. Anim. Ecol. 61:93–101.

Werren J. H. 1980. Sex ratio adaptations to local mate competition in a parasitic wasp. Science 208: 1157–1159.

Wylie H. G. 1976. Interference among females of *Nasonia vitripennis* (Hymenoptera: Pteromalidae) and its effect on sex ratio of their progeny. Can. Entomol. 108:655–661.

Received 1 November 1991, accepted 3 September 1992.

The Auk 109(4):937–938, 1992

A Comment: Estimating Absolute Densities of Flying Seabirds using Analyses of Relative Movement

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Recently, we described a method for correcting apparent densities of seabirds observed during at-sea surveys to eliminate error caused by the effect of flight speed and direction of the birds relative to speed and direction of the observation platform (a ship; Spear et al. 1992). We considered this method as previously undescribed. However, we are now aware that Gaston and Smith (1984; see also Gaston et al. 1987) had previously introduced a method very similar to ours, which they used to correct density estimates for the effect of bird movement during aerial surveys.

Literature Cited

Gaston, A. J., and G. E. J. Smith. 1984. The interpretation of aerial surveys for seabirds: Some ef-