Wilhelm Ludwig and his Contributions to Population Genetics

Janis Antonovics

This article reviews the life and work of the German biologist Wilhelm Ludwig (1901–1959), *whose contributions to population genetics have been largely ignored. Ludwig's work was a rich tapestry of population biology, spanning investigations into population growth, biological asymmetries, sex ratio, and paternity analysis. He was ahead of his time in explicitly combining the theory of population ecology and population genetics. His classic paper on annidation showed the possibility of population differentiation in the face of gene flow, and his early studies demonstrated the importance of selection in evolutionary change. Much of his work spanned the period of the Second World War in Germany, and interesting questions remain about his life during this turbulent period.*

Wilhelm Ludwig's paper 'Annidation as a Fifth Evolutionary Factor'[50], published in 1950, has been frequently quoted, both as the source of the term 'annidation' (meaning evolution of niche divergence) as well as for its major conclusion, namely that genetic differentiation and speciation can occur without spatial separation. It was the first study to demonstrate the maintenance of polymorphism by niche differentiation, and well ahead of its time in suggesting that adaptation to alternative niches could lead to sympatric speciation. The conclusions of this paper have subsequently been confirmed by numerous theoretical models (for a recent example, see Wilson and Turelli[65]), as well as by experimental and field observations (for a review see Thoday[66]).

Other than this single paper, the literature has been remarkably silent about Wilhelm Ludwig or any of his other possible achievements. According to the Citation Index, his annidation paper has been quoted over 30 times since 1955, but his other papers go unmentioned. Felsenstein[67] in his *Bibliography of Theoretical Population Genetics* lists only two other papers by Ludwig (Refs 30 and 44). Rensch[68], in his review of the evolutionary synthesis in Germany, mentions four of Ludwig's papers but merely ascribes to him the bland-sounding opinion that 'evolution can generally be explained by the analyzed factors of speciation, although other mechanisms are imaginable.'

My curiosity about Ludwig was not only fueled by a general interest in micro-differentiation and competition, but also by the rather uncanny way in which an example that he used in his seminal paper on annidation was a prelude to some of our work on genetic differentiation at metal mine boundaries nearly 20 years later (see Ref. 69). Thus, when discussing the possibility of genetic divergence in the face of gene flow, Ludwig[50] writes (p. 528): 'one thinks somewhat of two related grass species, one of which can germinate and grow on both bad and good soil, and the other which can germinate and grow only on the latter. Seeds are dispersed by the wind onto both types of soil . . .' It therefore came as an additional surprise and delight later to discover that one of Ludwig's very first papers[1] had been on the effects of heavy metals on *Paramecium*. This paper includes a thorough discussion of similar work on plants!

Three summers ago, while at the Botany School of Cambridge University, UK, I took the opportunity to research both the work and the life of Wilhelm Ludwig. I was aided considerably by discovering that a number of his papers were in R.A. Fisher's reprint collection, now housed in the library of the Cambridge Genetics Department. This formed a focus from which to work backwards and reconstruct as complete a bibliography as possible. This account is therefore largely based on Ludwig's scientific work and on an obituary written by Keilbach[70].

Wilhelm Ludwig's career as a scientist was highly productive and diverse, with over 130 publications between 1926 and 1960, spanning subjects as different as physiology, ecology and population genetics. But in spite of this diversity, it is clear that particular ideas and interests form a common thread throughout his work. His intellectual development can be traced back to his first paper[1] on the effects of heavy metals on *Paramecium*. This extensive study, and subsequent investigations on the growth and physiology of *Paramecium* and other protozoans[2,3], opened up his curiosity on two subjects that were to remain a passion for the rest of his life, and that led to his later interest in population genetics. The first area that intrigued him was the subject of resources, individual growth and population growth[4,5,22,24]. His initial paper on this topic[4] develops a theory of population growth under non-renewable resources. The model is based on the idea of a protozoan feeding on bacteria. The situation of infinite and constantly renewable resources is then treated as a special case and shown to agree with the formulations of Pearl[71]. Ludwig then shows that his theoretical models give a reasonable fit to previously published growth curves for protozoans.

His other main interest, in left- and right-handedness, came directly from the observation of the spiral locomotion of *Paramecium*; in particular, from the fact that *Paramecium* is predominantly, though

Wilhelm Ludwig

Janis Antonovics is at the Botany Dept, Duke University, Durham, NC 27706, USA.

not exclusively, 'left-handed'[6–8]. This led him to investigate all forms of left- and right-handedness in the natural world[10,11,14,17,21,23], and eventually other biological 'dichotomies', such as sex ratio[20] and behavioral choice[13,15,18,19].

Ludwig continually returns to these themes in later papers. He re-examines his theories of protozoan growth, taking into account autotoxic effects[28]. He continues his interest in sex ratio by examining the various factors that affect sex ratio[29], especially the increase in male-biased sex ratios during wartime[33–35,39,40,43,51]. And in his later work he again re-examines spiral locomotion[52] and left- and right-handedness[36,48,49,54,60,62].

Although Ludwig's first paper on population genetics[12] appears quite early in his career, it is not immediately obvious why he became interested in evolution and eventually became one of the strongest advocates of neo-darwinism. In general, his interest in population genetics would seem to be a natural extension of his earlier investigations on population growth and biological dichotomies (of which alternative alleles would be another example). Moreover, his involvement with *Paramecium* had extended to a consideration of its systematics[9], and his interest in locomotion asymmetries led him to examine these asymmetries in relation to protozoan phylogeny[6]. These papers hint at some interest in evolution. Moreover, a report published later[25] describes experiments that he had already started in 1933 to test (with subsequent negative results) lamarckian effects using *Drosophila* populations. However, it was probably the realization that his mathematical talents could easily be applied to these highly controversial issues of the time that led him into the field of theoretical population genetics.

His first paper on this subject[12] addresses a topic that had intrigued other theoretical evolutionists before him, including R.A. Fisher and J.B.S. Haldane. It was undoubtedly a topic of lively general debate. The subject was the efficacy of selection in causing the spread of mutations that gave only a very low selective advantage. In his paper, Ludwig develops equations for rates of gene frequency spread under selection, and shows that even small selective values can result in substantial changes in gene frequency. His model is particularly interesting in that it represents a special case of density-dependent selection. It is therefore one of the first, if not the first, that explicitly combines ideas of population regulation with gene frequency change. He assumes a constant population, with the result that mortality is proportional to offspring number. Selection then acts to offset this mortality, yet the level of selection and gene frequency in turn affect the overall mortality. He calculates the expected mortality of each genotype as a function of offspring number, the gene frequency, and the differential survival of the genotypes. This is then used to predict gene frequency change. Here (and later – see Ref. 30) he contrasts his model with that of Haldane[72], and points out that while the results are quantitatively similar, a major difference is that the offspring number will affect the rate of gene frequency change. The two models converge approximately when each individual produces two offspring.

In his discussion, Ludwig points out the importance of his results in showing how small selective advantages are sufficient to explain phyletic change. He also emphasizes a point made much later by Haldane[73] (see also Charlesworth[74]), namely, that increased adaptation need not result in greater population size, a result that follows clearly from his model. Expressed in modern-day jargon, Ludwig's model assumes that a selective advantage involves a decrease in the density-dependent mortality, rather than a decrease in density-independent mortality as assumed by classical population genetic models. Even now we have little direct evidence as to which assumption is more reasonable[75]. Ludwig's focus on density dependence has its source in his own earlier work on population growth models.

Ludwig's other papers on evolution form a broad-ranging medley. They include vigorous defenses of neo-darwinism[30,31,41,46,47,59,63] and considerations of particular issues such as character loss in cave dwellers[38,56] and evolution of adaptive traits in sterile workers of social insects[61]. They include other specific population genetic models showing, for example, how recurrent mutation greatly accelerates the spread of beneficial recessive genes[37]. He was aware of the major evolutionary issues being considered at that time; for example, in a book review[27] he assails the author for failing to quote Sewall Wright, and therefore failing to realize that gene frequencies would not change in a consistently directional manner following population subdivision. His other work on population genetics concerns problems of linkage analysis[16,26], inbreeding[42,44], pedigree analysis and genetic relatedness[32,45,57], and paternity analysis[53,55,58].

The now-classic paper on annidation appears in 1950, but a footnote indicates that the manuscript was completed in 1943 and subsequently revised in 1947. (There is mention[61] of a follow-up paper[64] on population size changes during annidation, but I have been unable as yet to locate this.) The conclusions of the paper are perhaps worth quoting verbatim:

> (1) Ecomutations can lead to differentiation of new races and species in *one locality and without spatial separation*.
> (2) Closely related species can *coexist permanently* within one region.
> (3) The average population ranges of the coexisting species *must be different*.
> (4) The spread of a new mutant, even race or species, by annidation can occur much *more rapidly* than by selection because the new types enter unoccupied niches, and don't have to gradually displace those already present as in the case of selection.
> (5) An ecomutation may have a strong competitive (selective) disadvantage, but it cannot be displaced from its own niche.
> (6) The origin of many selectively neutral and harmful mutations is therefore explainable, because they would not be possible in the competitive environment of the original form.
> (7) Ecomutations may also be responsible for the *extinction* of taxa if the habitat of a newly arisen mutation or immigrant species includes the particular niches of a long specialized species or species group.

Many of these conclusions are extensions of Gause's law. Indeed, Ludwig's theoretical argument begins, as in his earlier paper on selection[12], by considering two non-interbreeding mutants: he then shows that by simple extension his results can also be applied to interbreeding genotypes. In this recognition of a similarity between ecological and evolutionary theory, Ludwig was well ahead of his time. The paper was first cited, as far as I can tell, by Da Cuhna *et al.*[76], who refer to it as 'a little known paper'. It is most extensively cited by Mayr[77], who refers frequently to the 'Ludwig effect', or 'Ludwig's Theorem'. However, Mayr does not mention that the paper also argues strongly (as its main conclusion!) that sympatric divergence and speciation are likely outcomes of such a process. Subsequent citations seem often to have been derivative: beyond citing the source of the term 'annidation', the other conclusions of the paper have been ignored. It is not quoted in much of the later important theoretical work on multiple niche polymorphism[78] or sympatric divergence[79].

Looking at Ludwig's work as a whole, one gets the impression of a highly versatile, broad and productive scientist. It is not clear to me why his work has remained so unnoticed, but the reason is probably a combination of unusual circumstances. All of his work was in German, and much of it was published during the war, when German articles were unavailable. There may also have been a post-war antipathy towards reading such articles. Many of his reprints were received by R.A. Fisher in the mid 1950s, but Fisher did not read German (G. Cox, pers. commun.) and therefore may never have translated them. With the exception of a series on sex ratios with Charlotte Boost, most of his papers are single-authored. As a consequence, he does not seem to have left a large academic legacy. Population genetics is no longer a flourishing discipline in Germany.

The brief obituary of Ludwig[70] tells us more about his life. He was born in 1901 of Austrian nationality. He studied Biology and Mathematics in Leipzig, Freiburg and Kiel. He obtained his Doctor of Philosophy with J. Meisenheimer in Leipzig, and then worked as an assistant with B. Klatt in Halle. There he obtained a lectureship in 1930, and a professorship just prior to the war. He also became a German citizen. In 1941, as a result of the decisions of 'those in responsibility', he left Halle, and moved to a paid lectureship in Mainz. During the war he entered the Luftwaffe and was a prisoner of war. After the war he returned to Halle as Professor. In 1948 he became Professor and Director of the Zoological Institute, University of Heidelberg. He died in 1959 during a meeting of the German Biometric Society in Leipzig.

Many intriguing questions remain about his life and work. Certainly, if the reader has any other information on Wilhelm Ludwig I would be grateful to receive it. What was it that made him a fervent champion of darwinism? What influence did he have after the war, and why, in spite of his work, was there in Germany almost a total demise of population genetics as a science? He lived through some of the most turbulent times of this century. It is remarkable that he remained academically active throughout wartime Germany, entered or was drafted into the air force, was imprisoned, and then returned to an academic appointment in East Germany. From there he ended up at one of the most prestigious universities in West Germany. One cannot but wonder how all these events transpired.

In many ways Wilhelm Ludwig's work has much in common with that of our more familiar and accessible heroes such as Haldane, Fisher or Wright. It is characterized by enormous originality, biological understanding and intellectual breadth. And above all, it resulted in major contributions to evolutionary theory, many of which were far ahead of their time.

Acknowledgements

I am grateful to Gustav Fischer Verlag for permission to reproduce the photograph, and to Dr Charlotte Boost for providing the original. I would also like to thank Prof. Dr V. Storch, Dr C. Boost, Prof. Dr R. Keilbach and Dr R. Wette for insight and extensive information on the life and work of W. Ludwig.

Selected bibliography*

1 Ludwig, W. (1927) *Zeitschrift für vergleichende Physiologie* 6, 623–687 [The causes of extreme toxicity of heavy metal ions as well as of impurities in water and glass on *Paramecium aurelia*]

2 Ludwig, W. (1928) *Archiv für Protistenkunde* 62, 12–40 [The basal metabolism of *Paramecium caudatum* Ehrbg. A contribution to the question of the function of the contractile vacuoles]

3 Ludwig, W. (1928) *Zoologischer Anzeiger* 76, 273–285 [Permeability and water exchange in *Noctiluca miliaris*]

4 Ludwig, W. (1928) *Biologia* 4, 351–376 [On the functional relationship between population density, nutrient supply, and division rate in Protista and on increase in population size in general]

5 Ludwig, W. (1929) *Biologisches Zentralblatt* 49, 735–758 [A comparative study of growth laws]

6 Ludwig, W. (1929) *Verhandlungen der Deutschen Zoologischen Gesellschaft* 1929, 203–214 [On preference for right and left in animals]

7 Ludwig, W. (1929) *Zeitschrift für vergleichende Physiologie* 9, 734–801 [Investigations on the spiral locomotion of lower organisms]

8 Ludwig, W. (1930) *Zeitschrift für vergleichende Physiologie* 13, 397–504 [On the theory of flagellar movement (dynamics, efficiency, energy balance)]

9 Ludwig, W. (1930) *Zoologischer Anzeiger* 92, 33–41 [On nomenclature and systematics of the genus *Paramecium*]

10 Ludwig, W. (1931) *Verhandlungen der Deutschen Zoologischen Gesellschaft* 1931, 213–219 [Wing position in firebugs (*Pyrrhocoaris apterus*)]

11 Ludwig, W. (1932) *Das Rechts–Links Problem im Tierreich und beim Menschen*, J. Springer, Berlin [The right–left problem among animals and man]

12 Ludwig, W. (1933) *Biologisches Zentralblatt* 53, 364–379 [The effect of selection on mutations of small selective value]

13 Ludwig, W. (1933) *Zeitschrift für wissenschaftliche Zoologie* 144, 469–495 [Lateral constancy of lower animals in experiments with one and two light sources. I. *Lymantria dispar* caterpillars]

14 Ludwig, W. (1933) *Forschungen und Fortschritte* 9, 254–255 [The right–left problem in biology]

15 Ludwig, W. (1934) *Verhandlungen der Deutschen Zoologischen Gesellschaft* 1934, 27–34 [On a new form of animal behavior in experiments with one and several light sources]

16 Ludwig, W. (1934) *Zeitschrift für induktive Abstammungs- und Vererbungslehre* 67, 58–95 [On the numerical relationships of cross-over values with one another]

17 Ludwig, W. (1934) *Forschungen und Fortschritte* 10(22), 280–281 ['Surrogate investigations' on human sidedness using animal subjects]

18 Ludwig, W. (1934) *Zeitschrift für wissenschaftliche Zoologie* 146, 193–235 [Lateral constancy of lower animals in experiments with one and two light sources. II. Menotaxis as a cause of lateral constancy]

19 Ludwig, W. (1934) *Forschungen und Fortschritte* 10(26), 325–326 [The light compass movement of animals]

20 Ludwig, W. (1935) *Biologisches Zentralblatt* 55, 250–267 [Analogies between sex determination and the determination of asymmetries (the problem of right–left)]

21 Ludwig, W. (1936) *Verhandlungen der Deutschen Zoologischen Gesellschaft* 1936,

*A full bibliography is available on request from the author.

21–73 [The determination and inheritance of forms of asymmetry (the problem of right–left)]
22 Ludwig, W. (1937) *Zeitschrift für vergleichende Physiologie* 24, 319–342 [Body size, asymmetry, and energy balance]
23 Ludwig, W. (1937) *Wilhelm Roux Archiv für Entwicklungs-Mechanik der Organismen* 136, 294–312 [On the genesis of asymmetrical form in bed-bugs]
24 Ludwig, W. (1938) *Arbeiten aus dem biologisches Forschungsinstitutes* 10, 93–100 [On the relationship between body size, locomotion speed, heartbeat frequency, and other body frequencies in invertebrates]
25 Ludwig, W. (1938) *Zoologischer Anzeiger Supplementband* 11, 182–193 [A contribution to the question of the causes of evolution on a theoretical and experimental basis]
26 Ludwig, W. (1938) *Faktorenkoppelung und Faktorenaustausch bei normalen und aberranten Chromosomenbestand*, G. Thieme, Leipzig [Linkage and recombination in normal and aberrant chromosomes]
27 Ludwig, W. (1939) *Die Naturwissenschaften* 11, 177–179 [Book review of Reinig, W.F. (1938) *Elimination und Selektion*, G. Fischer, Jena]
28 Ludwig, W. and Boost, C. (1939) *Archiv für Protistenkunde* 92, 453–484 [On the growth of protozoan populations and the allelocatalytic effect]
29 Ludwig, W. (1939) *Medizinische Klinik* 19, 1–8 [Sex and sex determination in the animal kingdom]
30 Ludwig, W. (1939) *Zoologischer Anzeiger* 126, 209–222 [The concept of selective advantage and the speed of selection]
31 Ludwig, W. (1940) *Die Naturwissenschaften* 28, 689–705 [Selection and phylogeny]
32 Ludwig, W. and Boost, C. (1940) *Zeitschrift für menschlichen Vererbungs- und Konstitutionslehre* 24, 577–619 [Comparative evaluation of methods for the analysis of recessive inheritance in man]
33 Ludwig, W. and Boost, C. (1940) *Zeitschrift für Naturwissenschaften (Halle)* 94, 1–37 [On sex ratio in man. I. The effect of war and the standard of living]
34 Ludwig, W. and Boost, C. (1940) *Zeitschrift für Naturwissenschaften (Halle)* 94, 37–47 [On sex ratio in man. II. Its connection with the origin of biological statistics (in memory of J.P. Süssmilch, 1741)]
35 Ludwig, W. and Boost, C. (1941) *Zeitschrift für Kinderheilkunde* 62, 561–563 [The sex ratio of legitimate and illegitimate living and still-births during wartime]
36 Ludwig, W. (1941) *Die Naturwissenschaften* 28, 423–424 [Investigations on the right–left problem in *Hydroides norvegica*]
37 Ludwig, W. (1942) *Biologisches Zentralblatt* 62, 374–379 [On the role of mutation pressure in evolution]
38 Ludwig, W. (1942) *Biologisches Zentralblatt* 62, 447–455 [On the evolutionary explanation of characteristics of cave-dwelling animals by allelic elimination]
39 Ludwig, W. and Boost, C. (1942) *Biologia Generalis (Wien)* 16, 160–197 [On sex ratio in man. III. The cause of higher male mortality and its relationship to variation in the sex ratio]
40 Ludwig, W. and Boost, C. (1943) *Klinische Wochenschrift* 22, 189–194 [The dependence of the human sex ratio on hereditary and environmental influences, especially war]
41 Ludwig, W. (1943) in *Die Evolution der Organismen* (Heberer, G., ed.), pp. 479–520, G. Fischer, Jena [Selection theory]
42 Ludwig, W. (1944) *Zeitschrift für menschlichen Vererbungs- und Konstitutionslehre* 28, 278–312 [On inbreeding and kinship]
43 Ludwig, W. and Boost, C. (1947) *Zeitschrift für Naturforschung* 2b, 222–226 [On certation and sperm dimorphism in animals and man]
44 Ludwig, W. and Schelling, H.V. (1948) *Biologisches Zentralblatt* 67, 268–275 [The level of inbreeding in finite panmictic populations]
45 Ludwig, W. (1948) *Forschungen und Fortschritte* 24, 155–156 [Cousin-marriages and the Oedipus complex]
46 Ludwig, W. (1948) *Aufsätze und Reden der Senckenbergischen Naturforschenden Gesellschaft Frankfurt* 6, 1–36 [Darwin's theory of natural selection in a modern context]
47 Ludwig, W. (1948) *Universitas* 3, 941–952 [Darwinism in a modern light]
48 Ludwig, W. (1949) *Studium Generale* 2, 231–239 [Symmetry investigations in the animal kingdom]
49 Ludwig, W. (1950) *Zeitschrift für vergleichende Physiologie* 32, 464–467 [Body size, asymmetry, and energy balance III]
50 Ludwig, W. (1950) in *Neue Ergebnisse und Probleme der Zoologie (Klatt-Festschrift)*, pp. 516–537, Akademische Verlagsgesellschaft Geest and Portig, K-G., Leipzig [On the theory of competition. Annidation as the fifth evolutionary factor]
51 Ludwig, W. and Boost, C. (1951) *Zeitschrift für induktive Abstammungs- und Vererbungslehre* 38, 383–391 [On the relationship between parental age, litter size, and sex ratio in dogs]
52 Ludwig, W. and Schlicksupp, E. (1951) *Zoologischer Anzeiger* 147, 116–121 [The rotational direction of spiral locomotion of microorganisms and larvae as a help in phylogeny]
53 Ludwig, W. (1951) *Homo* 2, 55–58 [On the theory of the Essen-Möller method]
54 Ludwig, W. (1951) *Experientia*, 457–462 [Induced inversion of the asymmetry form in *Bacillus negroides*]
55 Ludwig, W. and Wartmann, R. (1952) *Deutsche Zeitschrift für gerichtliche Medizin* 41, 289–296 [Critical considerations on the genetic paternity test]
56 Ludwig, W. (1952) *Zeitschrift für induktive Abstammungs- und Vererbungslehre* 84, 462–479 [Studies on the evolutionary origin of characteristics of cave animals]
57 Ludwig, W. (1953) *Genus* 6, 3–10 [The frequency of four types of cousin-marriages]
58 Ludwig, W. (1954) *Wissenschaftlichen Zeitschrift der Karl-Marx-Universität Leipzig* 4, 13–19 [Probability theory arguments in paternity analysis]
59 Ludwig, W. (1954) in *Die Evolution der Organismen* (2nd edn) (Heberer, G., ed.), pp. 662–712, G. Fischer, Stuttgart [Selection theory]
60 Strangmann-Koehler, I. and Ludwig, W. (1954) *Zeitschrift für menschlichen Vererbungs- und Konstitutionslehre* 32, 219–258 [Investigations on the components of sidedness in man, especially of the veins]
61 Ludwig, W. (1958) *Zoologischer Anzeiger* 160, 244–247 [A note on the rapid evolution of abilities of workers in insect colonies]
62 Ludwig, W. and Wette, R. (1958) *Zeitschrift für menschlichen Vererbungs- und Konstitutionslehre* 34, 400–416 [On the classification of asymmetries and test of the left–right ratio, especially in man]
63 Ludwig, W. (1960) in *Hundert Jahre Evolutions-forschung* (Heber, G. and Schwanitz, W., eds), pp. 45–80, G. Fischer, Stuttgart [The present-day status of selection theory]
64 Ludwig, W. and Wartmann, R. Quoted as 'in press' in Ref. 61, but reference not found [Population dynamics during annidation]

References

65 Wilson, D.S. and Turelli, M. (1986) *Am. Nat.* 127, 835–850
66 Thoday, J.M. (1972) *Proc. R. Soc. London Ser. B* 182, 109–143
67 Felsenstein, J. (1981) *Bibliography of Theoretical Population Genetics*, Dowden, Hutchinson & Ross
68 Rensch, B. (1980) in *Evolutionary Synthesis* (Mayr, E. and Provine, W.B., eds), pp. 284–303, Harvard University Press
69 Antonovics, J., Bradshaw, A.D. and Turner, R.G. (1971) *Adv. Ecol. Res.* 7, 1–85
70 Keilbach, R. (1960) *Verhandlungen der Deutschen Zoologischen Gesellschaft* 1960, 535–536
71 Pearl, R. and Reed, L.J. (1920) *Proc. Natl Acad. Sci. USA* 6, 275–288
72 Haldane, J.B.S. (1924) *Trans. Cambridge Philos. Soc.* 23, 19–243
73 Haldane, J.B.S. (1953) *New Biol.* 15, 9–24
74 Charlesworth, B. (1971) *Ecology* 52, 469–474
75 Antonovics, J. and Via, S. (1988) in *Plant Population Biology* (Davy, A.J., Hutchings, M. and Watkinson, A.R., eds), pp. 185–203, Blackwell
76 Da Cuhna, A.B., Dobzhansky, T., Pavlosky, O. and Spassky, B. (1959) *Evolution* 13, 389–404
77 Mayr, E. (1963) *Animal Species and Evolution*, Harvard University Press
78 Levene, H. (1953) *Am. Nat.* 87, 331–333
79 Maynard Smith, J. (1966) *Am. Nat.* 100, 637–650

Letters to the Editor

TREE **welcomes correspondence. Letters to the Editor may address issues raised in the pages of *TREE*, or other matters of general interest to ecologists and evolutionary biologists. Letters should be no more than 300 words long, and any references should be cited in the style of *TREE* articles. All correspondence should be sent to The Editor, *Trends in Ecology and Evolution*, Elsevier Trends Journals, 68 Hills Road, Cambridge CB2 1LA, UK. The decision to publish rests with the Editor, and the author(s) of any *TREE* article criticized in a Letter will normally be invited to reply.**