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PERSPECTIVE

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ANIMAL FLIGHT MECHANICS IN PHYSICALLY VARIABLE GAS MIXTURES

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Summary

Empirical studies of animal flight performance have generally been implemented within the contemporary atmosphere. Experimental alteration of the physical composition of gas mixtures, however, permits construction of novel flight media and the non-invasive manipulation of flight biomechanics. For example, replacement of atmospheric nitrogen with various noble gases results in a tenfold variation in air density at a constant oxygen concentration. Such variation in air density correspondingly elicits extraordinary biomechanical effort from flying animals; hummingbirds and euglossine orchid bees hovering in such low-density but normoxic mixtures have demonstrated exceptionally high values for the mechanical power output of aerobic flight muscle. As with mechanical power, lift coefficients

during hovering increase at low air densities in spite of a concomitant decline in the Reynolds number of the wings. The physical effects of variable gas density may also be manifest in morphological and physiological adaptations of animals to flight across altitudinal gradients. Global variation in atmospheric composition during the late Paleozoic may also have influenced the initial evolution and subsequent diversification of ancestral pterygotes. For the present-day experimenter, the use of physically variable flight media represents a versatile opportunity to explore the range of kinematic and aerodynamic modulation available to flying animals.

Key words: aerodynamics, biomechanics, density, flight, hummingbirds, insects.

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Introduction

All volant animals fly within the earth's atmosphere, a mixture physically dominated by the relative concentrations of oxygen (20.95 %) and nitrogen (78.09 %). Minor atmospheric constituents, most importantly argon (0.9 %), carbon dioxide (0.03 %) and water vapor exert a much smaller influence on the physical features of the atmosphere. Of such features, air density and dynamic viscosity influence both the character and magnitude of aerodynamic forces acting on animal wings and bodies. In particular, the dimensionless parameter termed the Reynolds number ( $Re$ ) indicates the relative importance of inertial and viscous forces for both biological and technological objects moving within fluids (Vogel, 1994); lower values of  $Re$  indicate a greater influence of viscosity and reduced inertial effects. The  $Re$  varies in direct proportion to fluid density and object dimension, and in inverse proportion to the dynamic viscosity of the fluid.

Physical characteristics of hydrodynamic or aerodynamic flow around objects are equivalent when values of  $Re$  are the same. Object size or fluid composition can therefore be varied in the laboratory to model varying physical conditions dynamically. Such manipulations are a well-known component of the experimental repertoire in fluid biomechanics (Vogel,

1994), but have not been widely applied to *in vivo* studies. Given the anthropogenic context of modern laboratories, most experimental studies of flight mechanics have been conducted at densities near sea level, although some biomechanical studies of flight at simulated high altitude have been conducted with birds (e.g. Berger, 1974, 1978; see also Withers, 1981). Such experiments reduce total air pressure and, as a consequence, reduce the partial pressure of oxygen. Thus, organismal responses to such altitudinal simulations necessarily conflate biomechanical effects of reduced density with the physiological consequences of reduced oxygen availability.

By contrast, physical manipulations of density under normobaric conditions have rarely been used in studies of animal flight performance. Chadwick and Williams (1949; see also Chadwick, 1951; Sotavalta, 1952) utilized heliox (20.9 % oxygen/79.1 % helium) to investigate the density-dependence of wingbeat frequency for tethered insects. Because oxygen concentration does not differ between heliox and normal air, this manipulation directly alters aerodynamic flow over beating wings without reducing diffusive flux of oxygen. In the  $Re$  range relevant to much of animal flight ( $10^2$ – $10^4$ ), aerodynamic

Table 1. *Molecular/atomic mass and pure component viscosity for oxygen, nitrogen and the noble gases excluding radon*

Molecular species	Molecular/atomic mass (kDa)	Dynamic viscosity $\times 10^{-5}$ (Pa s)
Diatomic oxygen	32	2.03
Diatomic nitrogen	28	1.75
Helium	4	1.94
Neon	20.2	3.16
Argon	39.9	2.22
Krypton	83.8	2.57
Xenon	131.3	2.31
Halocarbon 116	138.1	1.44

Halocarbon 116 is a representative high-mass but low-viscosity synthetic molecule.

lift and drag are linearly proportional to air density. Induced drag and the associated induced power, by contrast, vary inversely with air density. Flight in variable-density gas mixtures therefore demands kinematic compensation to meet altered lift and power requirements. In particular, continuous variation over a wide range of air density permits the available range of kinematic modulation available to a flying animal to be expressed and quantified. Helium and allied elements conveniently provide the opportunity to implement just such a manipulation.

### Noble gases and experimental flight media

Helium is one of the six noble gases, elements with full outer electron shells that render the atom inert in normobaric biological contexts (Schreiner, 1968; Hamilton *et al.* 1970). Atomic masses of the noble gases vary substantially relative to molecular masses of present-day atmospheric constituents (Table 1). Replacement of atmospheric nitrogen with available noble gases (excluding the radioactive element radon) therefore permits a tenfold variation in air density at constant oxygen concentration (Table 2). Variation in dynamic viscosity may also be generated at constant density, albeit over a reduced range relative to the aforementioned density variation (Table 3). Simultaneous reduction or increase in oxygen concentration permits an even greater range of density and viscosity to be explored in the laboratory. Theory and formulae for estimating density and dynamic viscosity of variable composition gas mixtures are given in Reid *et al.* (1987).

Two additional physical properties of gases may influence animal flight performance in such experimental media. Oxygen and carbon dioxide diffusivity vary in inverse (but nonlinear) proportion to gas density; thermal conductivity exhibits a direct but again nonlinear relationship to density (see Reid *et al.* 1987). In insects, for example, tracheal diffusion can be substantially enhanced in heliox. The work of ventilatory respiration increases at higher densities; changes in air viscosity may also influence respiratory mechanics. Such effects potentially influence physiological interpretations of

Table 2. *Density ( $\rho$ ), dynamic viscosity ( $\mu$ ), kinematic viscosity ( $\nu$ ), and density and kinematic viscosity for experimental gas mixtures referenced to normobaric sea level density ( $\rho_0$ ) and kinematic viscosity ( $\nu_0$ ) of the contemporary atmosphere*

Composition	$\rho$ (kg m $^{-3}$ )	$\mu \times 10^{-5}$ (Pa s)	$\nu \times 10^{-5}$ (m $^2$ s $^{-1}$ )	$\rho/\rho_0$	$\nu/\nu_0$
21 % O $_2$ /79 % Xe	4.59	2.31	0.50	3.79	0.32
21 % O $_2$ /36 % Ar/43 % Kr	2.38	2.45	1.03	1.97	0.66
21 % O $_2$ /79 % N $_2$	1.21	1.86	1.55	1.0	1.0
21 % O $_2$ /39 % N $_2$ /40 % He	0.80	1.96	2.45	0.66	1.58
21 % O $_2$ /79 % He	0.41	2.16	5.26	0.34	3.39

Kinematic viscosity is defined as the dynamic viscosity divided by the density; the Reynolds number varies inversely with kinematic viscosity for a given object size and speed. A tenfold change in mixture density and kinematic viscosity is afforded by the use of noble gases, with much smaller variation in dynamic viscosity.

Table 3. *Density ( $\rho$ ), dynamic viscosity ( $\mu$ ), kinematic viscosity ( $\nu$ ), and density and kinematic viscosity for experimental gas mixtures referenced to normobaric sea level density ( $\rho_0$ ) and kinematic viscosity ( $\nu_0$ )*

Composition	$\rho$ (kg m $^{-3}$ )	$\mu \times 10^{-5}$ (Pa s)	$\nu \times 10^{-5}$ (m $^2$ s $^{-1}$ )	$\rho/\rho_0$	$\nu/\nu_0$
21 % O $_2$ /79 % N $_2$	1.21	1.86	1.55	1.0	1.0
21 % O $_2$ /26 % He/53 % Ar	1.21	2.23	1.85	1.0	1.19
21 % O $_2$ /55 % He/24 % Kr	1.21	2.53	2.11	1.0	1.36
21 % O $_2$ /69 % Ne/10 % Kr	1.21	2.80	2.33	1.0	1.50

A 50% increase in kinematic viscosity is afforded by the use of noble gases at constant mixture density.

flights at variable density, but are not of immediate concern for analysis of flight mechanics. However, the use of three-component hypoxic mixtures permits hypodense mixtures to be constructed with oxygen diffusivity and thermal conductivity equal to those of normal unmanipulated air. Thermal effects may also be offset through compensation by changes in ambient air temperature.

### Animal flight performance under hypodense conditions

Hovering flight is an extremely demanding aerodynamic and energetic task, yet hovering insects and birds are often capable of ascending flight indicative of supplemental power reserves. The magnitude of these reserves is difficult to evaluate because such performance is typically not subject to experimental control. Furthermore, intrusive experimental manipulations such as tethering and weight addition may adversely affect flight biomechanics as well as the behavioral motivation to fly. To circumvent these difficulties, Dudley (1995) used heliox as a flight medium to demonstrate dramatic increases in lift and power output of hovering orchid bees relative to flight in normal air. Stroke amplitude increased significantly in heliox while wingbeat frequency was unchanged;  $Re$  of the wing chord decreased on average by 41%. Although lift performance of airfoils generally degrades at lower  $Re$ , mean lift coefficients in heliox increased significantly relative to values for hovering in normal air.

Reduced-density techniques were also recently used to evaluate limits to flight performance in ruby-throated hummingbirds (Chai and Dudley, 1995). Flight of hummingbirds is of general interest in that oxygen consumption and muscle power output during hovering represent the highest known mass-specific values for these quantities in vertebrates (Suarez, 1992). Limits to locomotor capacity of hovering were unequivocally indicated by aerodynamic failure at low densities less than half that of air at sea level. Hummingbirds demonstrated considerable power reserves, with muscle mass-specific power (assuming perfect elastic energy storage) averaging from  $98 \text{ W kg}^{-1}$  in normal air to a maximum value of  $133 \text{ W kg}^{-1}$  prior to aerodynamic failure; muscle efficiency remained approximately constant at 10%. As with the orchid bees flying in heliox, modulation of power output was attained primarily through variation in wing-stroke amplitude. Mean lift coefficients required for flight increased at lower densities (as with orchid bees), in spite of an attendant decline in the  $Re$  (Fig. 1).

Aerodynamic failure for hovering hummingbirds occurred at stroke amplitudes near  $180^\circ$ , suggesting a simple geometrical constraint on performance. Subsequent density reduction trials with hyperoxic but hypodense mixtures (35% oxygen/balance helium and nitrogen) have similarly resulted in failure to sustain hovering when stroke amplitude approaches  $180^\circ$  (P. Chai and R. Dudley, unpublished data). Moreover, this aerodynamic failure occurs at gas densities and rates of mechanical and metabolic power production statistically equivalent to values in the aforementioned heliox

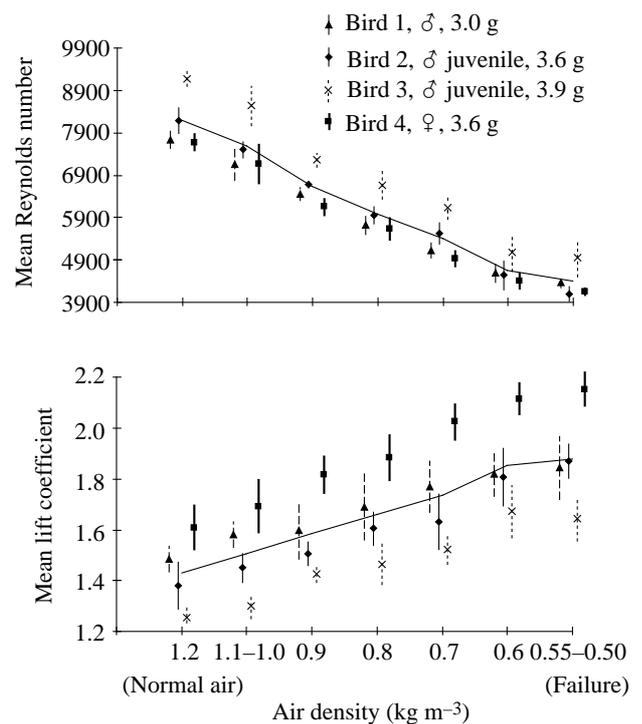


Fig. 1. (A) Mean Reynolds number ( $\pm 1$  s.d.,  $N=3-37$ ) of the wing chord in hovering flight and (B) mean lift coefficients ( $\pm 1$  s.d.,  $N=3-37$ ) required for flight by ruby-throated hummingbirds (*Archilochus colubris*) in normoxic density reduction trials (see Chai and Dudley, 1995, for methods).

experiments. This result indicates that oxygen supply does not, in this particular context of hovering flight, constrain energetic performance. This conclusion is corroborated by respiratory supply of normal air through a feeder mask when hummingbirds are aerodynamically challenged by hypodense heliox mixtures; failure invariably occurs at high values of the stroke amplitude (P. Chai and R. Dudley, unpublished data).

Muscle mass-specific power expended by euglossine bees in heliox ( $130-160 \text{ W kg}^{-1}$ ), as well the maximum value for hummingbirds ( $133 \text{ W kg}^{-1}$ ), suggest that a proposed maximum capacity of  $100 \text{ W kg}^{-1}$  for fast aerobic muscle (Josephson, 1993) does not apply, at least not to flying animals. The muscle mass-specific power output of one euglossine species (*Eulaema meriana*, approximately 820 mg body mass) also exceeds the maximum values derived for the much larger hummingbirds (3–3.9 g), an allometric result opposite to that derived from results of load lifting studies (see Ellington, 1991b). Further non-invasive studies with additional hovering taxa are required, however, to test the generality of this result; phylogenetic controls are also required to differentiate between possibly variable allometries of synchronous and asynchronous muscle. Interestingly, orchid bees in heliox exhibit stroke amplitudes of  $136-152^\circ$  and never attain the postulated constraint of  $180^\circ$ . It should also be emphasized that the power estimates for orchid bees and hummingbirds in heliox are minimum

estimates of mechanical power expenditure, as these values assume perfect elastic storage of wing inertial energy (see Ellington, 1984). Less efficient elastic storage within the flight apparatus would substantially increase power expenditure in both taxa. Finally, orchid bees were capable of vertical ascent in heliox, indicating supplemental power reserves even when flying in heliox (Dudley, 1995).

### Ecological and evolutionary correlates of variable air density

Sea-level density of air at 20 °C is about  $1.21 \text{ kg m}^{-3}$ , decreasing to  $0.95 \text{ kg m}^{-3}$  at 2000 m elevation and  $0.74 \text{ kg m}^{-3}$  at 4000 m. Such density reduction across altitudinal gradients (and parallel decline in oxygen partial pressure) may significantly influence flight-related morphology, physiology and distribution of insects (Mani, 1962, 1968). One bumblebee species, for example, has been recorded at altitudes as high as 5600 m near Mount Everest (Williams, 1985). To date, altitudinal correlates of insect flight mechanics have been not been demonstrated. Biomechanical influences of altitudinal density gradients have, however, been convincingly shown in behavioral and energetic studies of hummingbirds. Power expenditure of hummingbirds is increased at reduced total pressure (Berger, 1974). As elevation increases, hummingbird species exhibit interspecifically both longer wings and lower wing disc loadings in order to reduce induced power requirements, the predominant avenue of energetic expenditure during hovering (Feinsinger *et al.* 1979; Epting, 1980). Interspecific comparisons of all sympatric bird taxa also demonstrate longer wings at higher altitudes (see Rand, 1936; Traylor, 1950; Hamilton, 1961; Mayr, 1963), possibly reflecting a direct morphological response to the energetic demands of flight. Despite the doubly adverse effects of reduced oxygen availability and air density, high-altitude flights of birds are well-known and demonstrate the physiologically enhanced respiratory system of birds relative to other vertebrates (Faraci, 1991). In laboratory contexts, covariation of density and oxygen concentration in noble gas combinations will permit physiological and aerodynamic consequences of high-altitude flight to be decoupled and systematically elucidated.

Paleoatmospheres may also have been characterized by variation in physical properties such as density and viscosity. In particular, geophysical models suggest the existence of a late Paleozoic oxygen pulse in which oxygen concentrations climbed steadily from the late Devonian onwards, to reach 35 % by the Upper Carboniferous, and then declined to 15 % by end-Permian (Bernier and Canfield, 1989). Because nitrogen partial pressure is thought to have been constant throughout earth's history (Holland, 1984; Budyko *et al.* 1985), the late Paleozoic oxygen pulse indicates a parallel increase in atmospheric density at a time when protopterygotes were first evolving and subsequently diversifying (Graham *et al.* 1995). Changes in dynamic viscosity of the atmosphere, by contrast, would have been

much less pronounced. Biotically, the late Paleozoic increase in oxygen levels correlates temporally with arborescence in plants, the origin of insect flight and the invasion of land by tetrapods (Graham *et al.* 1995).

From the perspective of the origin of flight, enhanced lift production on articulated proto-winglets would have been an immediate consequence of elevated atmospheric density in the late Paleozoic; upwards shifts in the *Re* may also have been advantageous for generation of lift relative to drag (see Ellington, 1991a). Relaxed diffusional constraints in the tracheal system also permitted the evolution of Carboniferous gigantism in diverse insect orders as well as in other arthropods (Graham *et al.* 1995). Intriguingly, the Permian decline in oxygen levels may have contributed to the dramatic end-Permian disappearance of giant arthropod taxa. To date, paleontological data have been insufficient to trace within-lineage correlations between body size and estimated oxygen concentrations. However, experimental studies of both insect growth and flight metabolism under hyperoxic conditions provide interesting contemporary perspectives for reconstruction of protopterygote paleophysiology. Similarly, physical models of early pterygote insects (e.g. Flower, 1964; Wootton and Ellington, 1991) could advantageously be flight-tested in gas media that physically simulate postulated Paleozoic atmospheres.

### Conclusions

Inherent to all empirical studies of animal flight are the characteristics of the medium within which experimental subjects are flying. With the exception of reduced total pressure, however, physical features of the flight medium have received little experimental attention. The ease and range of manipulations provided by noble gas substitutions provide ample opportunity for non-invasive evaluation of the range and potential limits to animal flight performance. Most importantly, such experiments can be implemented on free-flying animals. In insects, for example, tethered simulations of flight can potentially induce behavioral, mechanical and metabolic deviations relative to free flight performance. Study of free-flying insects in physically variable media avoids artifactual problems of tethering while simultaneously permitting direct experimental control over the characteristics of aerodynamic flow. Similarly, changes in the force balance of flying animals are difficult without recourse to such intrusive methods as weight attachment (manipulation of the gravitational constant is not at present an experimental possibility, although centrifuges may be applicable in this context). By studying the performance of animals flying in novel gaseous media, a wide range of biomechanical performance can be evaluated that may otherwise be unavailable for study by the laboratory-based experimenter. These results are of direct relevance to our understanding of maximal performance, a locomotor feature for which evolution may well select during both mate choice and predator-prey interactions between volant organisms.

## References

- BERGER, M. (1974). Energiewechsel von Kolibris beim Schwirflug unter Höhenbedingungen. *J. Orn.* **115**, 273–288.
- BERGER, M. (1978). Ventilation in the hummingbirds *Colibri coruscans* during altitude hovering. In *Respiratory Function in Birds, Adult and Embryonic* (ed. J. Piiper), pp. 85–88. Berlin: Springer Verlag.
- BERNER, R. A. AND CANFIELD, D. E. (1989). A new model for atmospheric oxygen over Phanerozoic time. *Am. J. Sci.* **289**, 333–361.
- BUDYKO, M. I., RONOVA, A. B. AND YANSHIN, A. L. (1985). *History of the Earth's Atmosphere*. Berlin: Springer-Verlag.
- CHADWICK, L. E. (1951). Stroke amplitude as a function of air density in the flight of *Drosophila*. *Biol. Bull. mar. biol. Lab., Woods Hole* **100**, 15–27.
- CHADWICK, L. E. AND WILLIAMS, C. M. (1949). The effects of atmospheric pressure and composition on the flight of *Drosophila*. *Biol. Bull. mar. biol. Lab., Woods Hole* **97**, 115–137.
- CHAI, P. AND DUDLEY, R. (1995). Limits to vertebrate locomotor energetics suggested by hummingbirds hovering in heliox. *Nature* **377**, 722–725.
- DUDLEY, R. (1995). Extraordinary flight performance of orchid bees (Apidae: Euglossini) hovering in heliox (80% He/20% O<sub>2</sub>). *J. exp. Biol.* **198**, 1065–1070.
- ELLINGTON, C. P. (1984). The aerodynamics of hovering insect flight. VI. Lift and power requirements. *Phil. Trans. R. Soc. Lond. B* **305**, 145–181.
- ELLINGTON, C. P. (1991a). Aerodynamics and the origin of insect flight. *Adv. Insect Physiol.* **23**, 171–210.
- ELLINGTON, C. P. (1991b). Limitations on animal flight performance. *J. exp. Biol.* **160**, 71–91.
- EPTING, R. J. (1980). Functional dependence of the power for hovering on wing disc loading in hummingbirds. *Physiol. Zool.* **53**, 347–357.
- FARACI, F. M. (1991). Adaptations to hypoxia in birds: how to fly high. *A. Rev. Physiol.* **53**, 59–70.
- FEINSINGER, R., COLWELL, R. K., TERBORGH, J. AND CHAPLIN, S. B. (1979). Elevation and the morphology, flight energetics and foraging ecology of tropical hummingbirds. *Am. Nat.* **113**, 481–497.
- FLOWER, J. W. (1964). On the origin of flight in insects. *J. Insect Physiol.* **10**, 81–88.
- GRAHAM, J. B., DUDLEY, R., AGUILAR, N. AND GANS, C. (1995). Implications of the late Palaeozoic oxygen pulse for physiology and evolution. *Nature* **375**, 117–120.
- HAMILTON, R. W., COHEN, J. D., DOEBBLER, G. F., EXPOSITO, L. F., KING, J. M., SMITH, K. H. AND SCHREINER, H. R. (1970). Biochemical and metabolic effects of a six-month exposure of small animals to a helium–oxygen atmosphere. *Space Life Sci.* **2**, 57–99.
- HAMILTON, T. H. (1961). The adaptive significances of intraspecific trends of variation in wing length and body size among bird species. *Evolution* **15**, 180–195.
- HOLLAND, H. D. (1984). *The Chemical Evolution of the Atmosphere and Oceans*. Princeton: Princeton University Press.
- JOSEPHSON, R. K. (1993). Contraction dynamics and power output of skeletal muscle. *A. Rev. Physiol.* **55**, 527–546.
- MANI, M. S. (1962). *Introduction to High Altitude Entomology*. London: Methuen and Co. Ltd.
- MANI, M. S. (1968). *Ecology and Biogeography of High Altitude Insects*. The Hague: Dr W. Junk N. V. Publishers.
- MAYR, E. (1963). *Animal Species and Evolution*. Cambridge: Harvard University Press.
- RAND, A. S. (1936). Altitudinal variation in New Guinea birds. *Am. Mus. Novit.* **890**, 1–14.
- REID, R. C., PRAUSNITZ, J. M. AND POLING, B. E. (1987). *The Properties of Gases and Liquids* (4th edn). New York: McGraw-Hill.
- SCHREINER, H. R. (1968). General biological effects of the helium–xenon series of elements. *Fedn Proc. Fedn Am. Socs exp. Biol.* **27**, 872–878.
- SOTAVALTA, O. (1952). Flight-tone and wing-stroke frequency of insects and the dynamics of insect flight. *Nature* **170**, 1057–1060.
- SUAREZ, R. K. (1992). Hummingbird flight: Sustaining the highest mass-specific metabolic rates among vertebrates. *Experientia* **48**, 565–570.
- TRAYLOR, M. A. (1950). Altitudinal variation in Bolivian birds. *Condor* **52**, 123–126.
- VOGEL, S. (1994). *Life in Moving Fluids: The Physical Biology of Flow*. Princeton: Princeton University Press.
- WILLIAMS, P. H. (1985). A preliminary cladistic investigation of relationships among the bumble bees (Hymenoptera, Apidae). *Syst. Ent.* **10**, 239–225.
- WITHERS, P. C. (1981). The effects of ambient air pressure on oxygen consumption of resting and hovering honeybees. *J. comp. Physiol. B* **141**, 433–437.
- WOOTTON, R. J. AND ELLINGTON, C. P. (1991). Biomechanics and the origin of insect flight. In *Biomechanics in Evolution* (ed. J. M. V. Rayner and R. J. Wootton), pp. 99–112. Cambridge: Cambridge University Press.