

Index

- adaptive neutrality, of melanism, 26
- Adélie Penguin (*Pygoscelis adeliae*), 30
- age distribution, 124, 126, 275: geometric, 124, 126
- age at maturity
 - of Arctic Skua, 14, 130, 131, 132–6, 140, 279; and phenotypes, 132, 133–5, 140
 - natural selection of, 132
 - of Wandering Albatross, 133
- aggressive behaviour, *see* agonistic behaviour
- agonistic behaviour
 - of Arctic Skuas: *Aggressive Upright* posture, 151, 152, 155; in defence of territory, 146–51, 160, 164; towards different intruders, 160; *Intimidated Upright* posture, 151, 152; the *Jump*, 147–9; the *Long Call*, 150; *Pursuit Flights*, 147; the *Short Call*, 150; the *Swoop*, 146–9; towards a stuffed Bonxie, 11; the *Yelp*, 150
- Alaska,
 - Arctic Skuas of, 37
- Albon, S.T., 190, 310
- Alca torda*, *see* Razorbill
- analysis of χ^2 (chi-squared), 53–5, 134–5, 252, 254, 292: of assortative mating, 301–4; null hypothesis of, 301, 303
- analysis of variance: 285–90: of environmental and genetic effects, 111–2; *F* ratio of, 195, 288, 289; mean squares in, 195, 288–9; null hypothesis of, 195, 196, 288; orthogonal, 96–7, 196; of regression, 115
- Andersson, M., 60, 61, 63, 64, 74, 75, 76, 77, 78, 79, 146, 173, 309
- androgen, 212
- Anser caerulescens*, *see* Lesser Snow Goose
- Anxolabehere, D., 293, 311
- apostatic selection: of Arctic Skuas as predators, 28, 67–9; frequency-dependence of, 67, 69
- Arctic Foxes, predation on Arctic Skuas, 28
- Arctic Tern, 46, 60, 62: agility in flight of, 63; on Foula, 63; migration of, 48
- Argus pheasant, 182, 187
- Arnason, E., 28, 60, 64, 65, 67, 68, 69, 70, 71, 72, 309
- Ashkenazi, Shoshana, xv, 34
- assortative mating, 187, 188, 215, 238–43, 255–9, 263, 291–308
 - analysis of data of, 297–308; and χ^2 , 301–4
 - in Arctic Skua, 215, 242, 243, 256–9, 292, 304–6
 - correlation between mates in, 295–6, 298
 - evolution of, 239–40, 255, 259, 263, 291; by ethological isolation, 291
 - genetic models of, 238–43
 - of Lesser Snow Goose, 239, 243, 292; by imprinting, 230, 292
 - and polymorphism, 291
- assortment of phenotypes, 239, 292
- atmospheric pollution, and melanism in *Biston betularia*, 27–8
- auks, 37, 43, 60
- BTO (British Trust for Ornithology), 16
- banding, *see* ringing
- Barlow, G.W., 161, 162, 309
- Barrington, R.M., 39, 309
- Baxter, E.V., 40, 41, 309
- Bear Island, Arctic Skuas on, 50
- behaviour, *see* agonistic behaviour, sexual behaviour
- Bengtson, S.A. 33, 37, 309
- Berry, R.J., xiv, 309
- bird of paradise, 182
- Bishop, J.A., 28, 309
- Biston betularia*
 - melanism of, 27–8; and atmospheric pollution, 28
 - relative fitness of melanistic, 28
- Blue Tit, 46

316 *Index*

- Bonxie (*Catharacta skua*)
breeding dates of, 43–4, 81; on Fair Isle, 9, 44, 81; on Foula, 1, 39, 43–7; on Hermaness, 1, 40, 43, 81, 266
in competition with Arctic Skuas, 43–7, 277; for territories, 43–4, 160, 266
evolutionary relationships to other skuas, 30
measurements of, 29
nests of 9
predation on Arctic Skuas by, 44–7, 92, 173, 266, 277
rate of increase of, 46, 266
Bourne, W.R.P., 37, 41, 309, 310
Brathay Exploration Group, 34, 39
breeding date
of Arctic Skua, 18–9, 43, 81–3, 86, 115, 194–203, 245, 247, 254, 261–2; and clutch size, 86; of established pairs, 81–3; and fledging period, 93–4; fitness function of, 115, 175–6, 203–6; and male experience, 200–1, 261–2; of males in new pairs, 81–2, 194–203, 245, 247; and preferential mating, 245; of second-year pairs, 198–200; skewed distribution of, 18, 254
of Bonxies, 43–4, 81
and female choice, 192, 245
measured by hatching date, 19, 89–90, 247
and reproductive success, 166, 173, 191
and territory size, 165, 169–72, 174–9
breeding range, of Arctic Skua, 1, 37, 38; in Northern Hemisphere, 37, 38; in Spitzbergen, 1, 37
breeding season
of Arctic Skua, 18–9, 81–4
extended season, of feral pigeon, 23–7, 165, 212; and melanism, 23–7, 165, 212
Bressay, Arctic Skuas of, 1
British Trust for Ornithology (BTO), 16
Broad, Roger, 2, 93;
broodiness, of Arctic Skua, 12
Brown, J.L., 72, 73, 309
Bulmer, M.G., 124, 132, 275, 309
Burger, J., 145, 159, 309
butterwort (*Pinguicula vulgaris*), 8
Caithness, Arctic Skuas in, 50
Calidris melanotos (Pectoral Sandpiper), 162
catching Arctic Skuas, xiv, xv, 4, 10–4, 19, 157; in clap-nets, xv, 12, 157; dummy eggs for, 13; fledglings, 19; in funnel traps, xiv, 12, 13; in mist net, 11
Calluna vulgaris (heather), 4
calorific value, of food of Arctic Skua, 69–70
- Cardamine pratensis* (lady's smock), 8
Catharacta maccormicki, *see* McCormick's Skua
Catharacta skua, *see* Bonxie, Southern Skua
Cepaea nemoralis, 67, 267
Charlesworth, B., 232, 233, 309
Charlesworth, D., 232, 233, 309
 χ^2 (chi-squared), 53–5, 134–5, 204–5; analysis of, 53–5, 134–5, 252, 254, 292, 301–4
chicks
of Arctic Skuas, 19, 21–3; with barred plumage, 21; death of, by drowning, 91; first flights of, 79, 92; fledgling of, 19, 82–4, 92
choice, *see* female choice
circadian oscillator, 26
Clarke, B., 67, 309
Clarke, C.A., 28, 309
cline
in Arctic Skua, 10, 47–59, 260, 269–70; map of, 51; movement of 55–8; phenotypic frequencies of, 10, 50, 52–6, 260
balanced by selection and migration, 47–8, 269–70
balanced by selection pressures, 48, 57, 58, 59, 269–70
and gene flow, 47–8, 270
neutral zone of, 50, 55, 57–8, 269–70
S-shaped curve of, 50, 53, 57, 270
as wave of advance, 56, 57, 269
cloaca, of Arctic Skua, 18
clutch, of Arctic Skua, 17; and breeding date, 86; size of, 85, 86
Clutton-Brock, T.H., 190, 310
coefficients
of sexual selection, *see* sexual selective coefficients
of natural selection, *see* selective coefficients
cohort, 14–15, 120, 123, 124, 275
colonial breeding
and distribution of food, 73
of terns, 73
Columba livia, *see* feral pigeon
Common Tern, 60, 62, 63; agility in flight of, 63
competition
of Arctic Skuas and Bonxies, 43–7, 277; for territories, 43–4, 160, 266
and *see* male competition
Cooch, F.G., 239, 310
Cooke, F., 239, 291, 292, 304, 310
copulation, of Arctic Skua, 156–8
correlation
in assortative mating, 295–6, 298

Index

317

- correlation (*cont.*)
 - of breeding date and territory size, 170, 171, 176, 178: homogeneity of, 171; hypothetical, 176, 178
 - of parents and offspring, 117
- cotton grass (*Eriophorum angustifolium*), 8
- courting males, 211, 212, 215: female encounters with, 211
- courtship, *see* male courtship, sexual behaviour
- Cramp, S., 37, 310
- Crook, J.H., 73, 310
- Crowberry (*Empetrum nigrum*), 4, 60: in diet of Arctic Skua, 60
- Dactylorhiza fuchsii* (spotted orchid), 8
- Darwin, Charles, 1, 14, 27, 152, 166, 172, 173, 180–4, 186, 187, 190, 193, 203, 208, 219, 263, 310
 - on natural selection, 14, 166, 180–4
 - on sexual selection, 14, 166, 180–4: in monogamous birds, 14, 152, 173, 191, 203, 208, 219, 263
- data records, of Arctic Skua: on nest record cards, 17, 194; on ring number cards, 15
- Davis, J.W.F., xiv, 2, 10, 11, 34, 39, 43, 44, 73, 85, 86, 89, 93, 125, 127, 129, 135, 136, 165, 166, 168, 169, 171, 176, 179, 212, 239, 275, 292, 304, 306, 307, 310, 313
- Davis, P.E., xiv, 1, 10, 101, 102, 103, 104, 105, 106, 309, 313
- Dawkins, R., 183, 310
- Dawson, W.R., 70, 312
- Dean, F.C., 37, 310
- death rate, *see* mortality
- defence, of territory of Arctic Skua, 146–51, 160, 164
- demography, of Arctic Skua, 10, 120–3, 136, 155, 265, 267
- diet, of Arctic Skua: of Crowberries, 60; in Norway, 76–9, 146; and territoriality, 74, 76–9
- Diomedea exulans* (Wandering Albatross), 133
- disassortative mating, 239, 291–308:
 - analysis of, 297–308; of Eleonora's Falcon, 243, 292, 307–8; of feral pigeon, 26, 212–3, 239, 243, 291–2, 306–7
- distraction behaviour, *see* injury feigning
- divorce, of mated Arctic Skuas, 154–5, 156, 199, 200
- Dixon, T.J., 41, 309
- domain of attraction, to gene fixation, 143
- dominance, defined, 216–7
- Dott, H.E.M., 41, 310
- Drosophila*, 190, 211: 'rare male' effect in, 190
- Dublin, L.I., 274, 310
- dummy eggs, for catching Arctic Skuas, 13
- ecology, population, 264–5
- Edge Land, Arctic Skuas in, 52
- Edwards, A.W.F., 248, 250, 310
- eggs, of Arctic Skua: hatching dates of, 18–9, 81–3; laying dates of, 81–2, 84
- Ehrman, L., 190, 211, 310
- eider ducks, 8
- Eleonora's Falcon (*Falco eleonorae*):
 - disassortative mating of, 243, 292, 307–8; melanism of, 23, 292
- Empetrum nigrum*, *see* Crowberry
- energetics, of Arctic Skua: and energy balance, 70–2; energy produced, 67–70; and energy used, 70
- equilibrium, genetic
 - defined, 218
 - with male competition, 235–6
 - with preferential mating, 218–22, 223–5, 251; and natural selection, 227–8, 229–31
- stability of, 219, 236, 251; and heterozygous advantage, 236
- unstable, 142–3, 268; and heterozygous disadvantage, 142, 268
- Eriophorum angustifolium* (cotton grass), 8
- estimates, maximum likelihood, 103, 104, 248–9, 253, 292, 294, 295–7: of female preferences, 249, 257–8, 268, 295–7
- evolution
 - adaptive, 27
 - of assortative mating, 240, 255, 259, 263, 291
 - of breeding date, 115
 - of early maturity, 133
 - of female preference, 116, 182–9, 214, 255, 259, 260, 263
 - of intelligence, 112
 - non-adaptive, 27
 - and protected polymorphisms, 267
 - of reproductive rate, 117
 - of sexual dimorphism, 180
 - of territoriality, 72, 74, 79, 173–4, 179; by sexual selection, 174, 179
- evolutionary relationships, of Arctic Skua, 30
- extermination, of Arctic Skuas on Fair Isle, 129, 130, 265
- F* ratio, 195, 288, 289
- FSH, *see* follicle-stimulating hormone
- Fabritius, H.E., 39, 310

318 *Index*

- Faeroe, Arctic Skuas in, 37, 57
 Fair Isle
 airstrip on, 2, 4, 41–3
 Arctic Skuas of, 1: colonization by, 2, 3;
 exponential increase of, 42, 121, 125,
 265; extermination of, 129, 130, 265;
 numbers of, 33, 41–3, 125; shooting of,
 1, 18, 42, 43, 127–31, 140, 155, 265
 bird observatory on, 8, 9
 Bonxies of, 9, 44, 81
 human population of, 4
 peat cutting on, 4
 plantacrubs of, 8
Falco concolor, 23
Falco eleonorae, *see* Eleonora's Falcon
 Falconer, D.S., 112, 113, 116, 310
 Farr, J.A., 190, 310
 feeding
 of Arctic Skua, 46, 60–9: energy yield of,
 69–72; and food defendability
 hypothesis, 74–80
 of Long-tailed Skua, 30
 female arousal, 210, *and see* female sexual
 response
 female choice, 181–2, 187, 191–3, 215, 232,
 243, 245–7, 255, 259–63
 in Arctic Skua, 215, 245, 255, 259–63:
 evidence for, 259–63
 and assortative mating, 215, 243, 255, 260
 of beautiful males, 182
 and breeding dates, 192, 245
 computer models of, 191–3, 245–7
 by response to sexual stimulation, 182,
 185
 female encounters, with courting males, 211
 female preference
 of Arctic Skua, 244–63: assortative,
 256–9, 304–6; estimates of, 249, 257–8,
 268, 295–7; for melanic males, 89, 245,
 247, 249, 257–8, 268
 assortative, 187, 188, 238–43, 291–3,
 295–7, 304–8
 estimation of, 231, 247–50, 292, 295–7
 evolution of, 116, 182–9, 214, 255, 259,
 260, 263: exponential rate of, 184, 186;
 genetic models of, 186–7
 models of, 245–55
 relative expression of, 185
 for supernormal stimuli, 185, 187–8
 for territorial quality, 183
 female sexual response
 inhibition of, 215, 239, 255: in assortative
 mating, 215, 239, 255
 shift in, 185
 to stimulation, 182, 211, 213
 to supernormal stimuli, 185, 187–8
 threshold of, 182, 210, 212, 214, 216, 250
 feral pigeon (*Columba livia*)
 disassortative mating of, 26, 212–3, 239,
 243, 291–2, 306–7
 melanism of, 23–7, 165, 212: and
 extended breeding season, 23–7, 165,
 212; and photoreponse, 24, 165, 212;
 and reproductive success, 26, 212
 photoperiodism of, 26, 212
 phenotypes of, 26, 306
 preferential mating of, 26, 165, 306–7
 fescue grass, 4
 Fetlar, Arctic Skuas of, 1
 Finland, Arctic Skuas in, 37, 53, 56–7
 Fisher, R.A., 56, 68, 183, 240, 269, 311
 combination of probabilities test of, 68,
 205
 on evolution of preference, 182, 184–7,
 250
 z transformation of, 171, 298
 fitness function, of breeding dates, 117,
 175–6, 203–6
 fledging, of Arctic Skua chicks, 19, 82–4, 92
 fledging period
 of Arctic Skua, 19, 82, 91–9: and
 breeding date, 93–4; and breeding
 experience, 94–7; of first and second
 chicks, 97–8; and phenotype, 98–9;
 standard deviation of, 93
 fledglings, of Arctic Skua, 82–3, 91
 follicle-stimulating hormone (FSH), 26
 food defendability hypothesis, 74–80
 Foula
 Arctic Skuas of, 1: exponential increase
 of, 44; numbers of, 34–6, 39–40, 43–7,
 125, 265, 266; predicted decline of, 45,
 278, 281
 Arctic Terns on, 63
 Bonxies of, 1, 39, 43–7
 founder effect, 259
Fratercula arctica, *see* Puffin
 French, J.M., 212
 frequency-dependent advantage
 apostatic, 66, 69
 of preferential mating, 192, 211–2, 232,
 268
 Fulmar, 23, 37: blue form of, 23
 Furness, B.L., 60, 67, 69, 311
 Furness, R.W., 34, 39, 44, 45, 46, 60, 67, 69,
 311
 Gannet, 37–8, 43
 gene flow, along Arctic Skua cline, 47–8, 57,
 269–70
 gene frequency, 57, 58, 142–4: defined, 109,
 217; at equilibrium, 218–25, 227–31,
 251, (and rate of convergence to), 219
 generation, 122

Index

319

- generation time (T), 122–3, 272, 273–4, 276
 genetic analysis
 of Arctic Skua matings, 100–8; with different phenotypic classifications, 106–8; model for, 101–4; with viabilities of phenotypes, 103–4
 genetic equilibrium, *see* equilibrium, genetic
 genetic interaction, 111–2
 genetic models
 of assortative mating, 238–43
 of evolution of female preference, 186–7
 of male competition, 232–6
 of preferential mating, 215–31
 genetic polymorphism, *see* polymorphism
 genetics
 of Arctic Skua phenotypes, 19, 100–10;
 and frequencies of phenotypes, 108–10;
 and viability of phenotypes, 103–4
 population, 264, 267
 genotypes
 of Arctic Skua, 100–10
 assortative mating of, 243
 in females, 228–9
 in models of preferential mating, 216, 222–5
 Gibson, R.M., 190, 310
 Glessner, S.F., 242, 311
 gonadotrophin, 26, 212
 Gordon, N.J., 40, 41
 Götmark, F., 74, 75, 76, 77, 78, 79, 146, 173, 309
 Goux, J.M., 293, 311
 Grant, B., 242, 311
 Grant, P.R., 60, 61, 62, 64, 65, 69, 70, 71, 72, 162, 309, 311
 Great Black-backed Gull, 37
 Great Skua (*Catharacta skua*), *see* Bonxie
 Great Tit, 46, 124, 125, 126, 132–3
 Greenland, Arctic Skuas in, 37
 group selection, 45
 Guillemot (*Uria aalge*), 37, 60, 78
 Guinness, F.E., 190, 310
 guppy (*Poecilia reticulata*), 188, 190:
 polygyny of, 190; polymorphism of, 190; ‘rare male’ effect in mating of, 190
 Haldane, J.B.S., 269, 311
 Hardy-Weinberg Law, 109, 217–9, 223, 225, 229, 236, 251
 Harris, M.P., 36, 37, 38, 46, 311
 Harvey, P.H., 190, 310
 Hasegawa, M., 162, 311
 hatching
 of Arctic Skua eggs, 19; and dates of, 19, 89–90
 heather (*Calluna vulgaris*), 4
 heritability
 in Arctic Skua, 114–9; of breeding date, 114–5; of clutch size, 116–8; of fledging success, 117–9
 estimation of, 112–4; by regression of offspring and parents, 112–4
 of fitness, 116
 Hermaness
 Arctic Skuas on, 1, 43; numbers of, 40–1, 125, 266
 Bonxies on, 1, 40, 43, 81, 266
 Herring Gull, 43, 145, 159; territories of 145, 159
 heterozygous advantage, 236, 244, 260
 heterozygous disadvantage, 142, 267, 268; and unstable equilibrium, 142, 268
 Hilden, O., 37, 53, 56, 311
 hormones: androgen, 212;
 follicle-stimulating hormone, 26;
 gonadotrophin, 26, 212; luteinizing hormone, 26; melanophore-stimulating hormone, 26; testosterone, 164–5, 179
 Huxley, J.S., 182, 183, 311
 Iceland
 Arctic Skuas in, 33, 37, 52–5, 57, 67;
 numbers of, 33, 37, 52–5
 imprinting, 239, 291, 304
 incubation, of Arctic Skua, 12, 85–91; and broodiness, 12, 88; with three eggs in clutch, 118
 incubation period, of Arctic Skua, 85–91;
 and breeding experience, 88–9; of first and second eggs, 87–8; standard deviation of, 89; and phenotypes, 88–91
 injury feigning, of Arctic Skua, 6, 16, 84, 85, 160, 161
 intelligence, evolution of, 112
 Jackson, E.E., 10, 311
 Jan Mayen, Arctic Skuas on, 50, 52, 54
 Jourdain, F.C.R., 17, 314
 Karlin, S., 50, 211, 240, 242, 243, 269, 270, 311, 313
 Kettlewell, B., 28, 311
 Kimball, A.W., 135, 311
 Kinnear, Peter, 40
 Kittiwake, 43, 60, 78, 115, 140
 kleptoparasitism
 and apostatic selection, 66–9
 of Arctic Skua, 49, 60–6; and apostatic selection of phenotypes, 66–9; in attacks on Puffins, 60–6; in attacks on terns, 60–4; and duration of attacks, 63–4; in groups, 61; and success in attacks, 64, 65

320 *Index*

- LH, *see* luteinizing hormone
 Lack, D., 46, 72, 117, 311, 312
 lady's smock (*Cardamine pratensis*), 8
Lagopus lagopus scoticus (Red Grouse), 164–5
 Lasiewski, R.C., 70, 312
 Lesser Snow Goose (*Anser caerulescens*): assortative mating of, 239, 243, 292; imprinting of, 239, 292, 304; melanism of, 23
 Lewontin, R.C., 76, 183, 312
 likelihood, 247–50
 maximum, 247–9; estimates at, 103, 104, 248–9, 253, 292, 294, 295–7
 principle of, 248; and scientific inference, 248
 surface, 249
 likelihood surface, 249
 linkage, 26, 76, 78, 185
 and pleiotropic effect, 27
 in polymorphism of behavioural traits, 76, 78; of feeding and territoriality, 76, 78
 log likelihood
 maximization of, 248
 support in units of, 249, 250
 Long-tailed Skua (*Stercorarius longicaudus*): evolutionary relationships with other skuas, 30; feeding of, 30; measurements of, 29; northerly distribution of, 30; phenotypic frequencies of, 30; predation by, 30
 Lotka, A.J., 274, 310
 Lotka's equation, 272
 luteinizing hormone (LH), 26
 M.L. estimates, *see* estimates, maximum likelihood
 MSH, *see* melanophore-stimulating hormone
 macrogametes, 181
 Magoun, A.J., 37, 310
 male competition, 181, 182, 188, 208, 232–8, 244, 261–3
 in courtship, 232
 genetic models of, 232–6: with dominant and recessive phenotypes, 233–4; with each different genotype, 234–6; with natural selection, 236–8
 and male experience, 200–1, 261–2, 263
 male courtship, 182, 210–5, 250, 262: and androgen level, 212; of Arctic Skua, 215; competition in, 232; and disassortative mating, 213; female response to, 182, 211, 213, 214–5, 250
 male sex hormone, *see* testosterone
 mating preference, *see* female preference
 maturity, age at, *see* age at maturity
 Maxwell, A.E., 135, 312
 maximum likelihood, *see* likelihood, maximum
 Maynard-Smith, J., 291, 312
 McCormick's Skua (*Catharacta maccormicki*): evolutionary relationships with other skuas, 30; extreme range of, 30; measurements of, 29; specialized feeding of, 30
 mean squares, in analysis of variance, 195, 288–9
 measurements, of Arctic and other skuas, 29
 melanism
 adaptively neutral, 26
 of Arctic Skua: and melanic phenotypes, 9, 19–23, 47, 50, 52–7, 133, 137–9, 214; semi-dominance of, 19, 100, 216, 252, 254
 of *Biston betularia*, 27–8
 of Eleonora's Falcon, 23, 292
 of *Falco concolor*, 23
 of feral pigeon, 23–7, 165, 212: and extended breeding season, 23–7, 165, 212; and photoreponse, 24, 165, 212; and reproductive success, 26, 212
 of Lesser Snow Goose, 23
 as pleiotropic effect, 26, 28
 melanophore-stimulating hormone (MSH), 26
 microgametes, 181
 migration
 of Arctic Skua: 15, 32, 37, 47–50, 261, 265; annual, 48–50; along cline, 47–8, 261; estimates of, 48; across generations, 48, 261; to other colonies, 15, 48, 261, 265; numbers on, 32, 37
 of Arctic Tern, 48
 of genes, 47–8, 56, 57, 221
 mimicry, and adaptive evolution, 27
 Mirsky, P.J., 239, 310
 monogamous species, 14, 152, 173, 189–93, 210, 220, 222, 224, 227, 231, 232, 233, 234, 240
 monogamy
 compared with polygamy, 222, 224, 227, 234
 in models of assortative mating, 293
 Moodie, G.E.E., 188, 312
Mormoniella vitripennis, 242
 mortality (death rate)
 of Arctic Skua, 126, 127–31, 139–42, 155, 277–9; and phenotypes, 127, 128, 130–1; by shooting, 129, 130, 155
 constant, 124, 275
 in first year, 126–7, 278, 279
 Moss, R., 164, 314

Index

321

- moulting
 of Arctic Skua, 21
 energy for, 26
- Mousa, Arctic Skuas from, 48
- mouthbrooder fish (*Tilapia mossambica*), 161
- Murton, R.K., 24, 25, 26, 165, 212, 291, 306, 312
- mutations, 116, 218, 221
- NERC (Natural Environment Research Council), xiv, xv, 1
- Nardus stricta*, 4
- Natural Environment Research Council (NERC), xiv, xv, 1
- natural selection, 17, 123, 139–44, 172
 of age at maturity, 132
 of Arctic Skua phenotypes, 17, 139–44;
 189; and components of, 17, 139–44;
 with heterozygous disadvantage, 142
 by competition for resources, 173
 in opposition to sexual selection, 184–5,
 188–9
 for an optimum, 183
 of reproductive rates, 117
 of territoriality, 173–4
- Nature Conservancy, xv, 40
- Nei, M., 27, 312
- nest building, 158–9
- nests
 of Arctic Skuas, xv, 3, 4, 6: checking, 3, 4,
 8, 17, 82; distance between, 9;
 mapping, xv, 18, 162–3; marked by
 canes, 6, 8, 16, 82; record cards of, 17
 of Bonxies, 9
- net reproductive rate (R_o), 122–3, 130, 272,
 273, 274, 276, 279, 281
- Normal distribution, 205
- Northern Hemisphere
 breeding range of Arctic Skua in, 37, 38
 map of, 38
- Norway, Arctic Skuas in, 52: diet of, 76–9,
 146; territories of, 146
- Noss, Arctic Skuas on, 1, 40, 125: numbers
 of, 40, 125, 265, 266
- null hypothesis, 195, 196, 205: of analysis of
 variance, 195, 196, 288; of analysis of
 χ^2 , 301, 303
- O'Donald, P., 10, 39, 41, 53, 67, 73, 101,
 102, 103, 104, 105, 106, 125, 127, 135,
 136, 138, 165, 166, 168, 169, 171, 173,
 174, 176, 177, 179, 182, 185, 186, 187,
 192, 193, 196, 203, 206, 208, 211, 212,
 213, 216, 219, 225, 226, 231, 233, 239,
 240, 242, 243, 255, 257, 275, 286, 291,
 292, 294, 304, 306, 307, 309, 310, 311,
 312, 313
- Orkney, Arctic Skuas in, 50, 52, 54, 56, 57
- Owen, A.R.G., 142, 144, 313
- Owen, D.F., 33, 37, 53, 309
- pair formation, 152–3, 200: time required
 for, 200, 244
- passerine birds, 193
- peat cutting, on Fair Isle, 4
- peacock, 182, 187, 229
- Pectoral Sandpiper (*Calidris melanotos*), 162
- Pennie, I.D., 10, 39, 313
- Perdeck, A.C., xv, 145, 147, 150, 151, 152,
 155, 158, 177, 313
- Perrins, C.M., 124, 132, 275, 309
- Perry, R., 10, 40, 313
- Petit, C., 190, 313
- phenotypes
 of Arctic Skua: assortative mating of,
 242, 256–9, 304–6; change of, from
 chick to adult, 104–5; cline in
 frequencies of, 10, 50, 52–6, 260;
 fledging period of, 98–9; melanic
 (dark), 19, 20, 23, (intermediate), 19,
 20–3; non-melanic (pale), 19–20, 21;
 selective coefficients of, 141, 143,
 206–8, 263; territory size of, 165,
 166–8, 179
- photoperiodism
 of Arctic Skua, 11
 of feral pigeon, 26, 212
 in secretion of hormones, 26
- photoresponse
 of melanic pigeons, 24, 165, 212
 in secretion of hormones, 165:
 gonadotrophin, 165, 212; androgen,
 212
- Pinguicula vulgaris* (butterwort), 8
- Pitt, F., 41, 313
- plantacrubs, on Fair Isle, 8
- pleiotropic effect
 and linkage, 27
 melanism as, 26, 28
- pollution, *see* atmospheric pollution
- polygynous species, 189, 193, 211, 220, 222,
 224, 231, 232, 233, 234, 294
- polygyny,
 compared with monogamy, 222, 224, 227,
 234
- of guppy, 190
- in models of assortative mating, 293–4
- of ruff, 189
- polymorphism
 of Arctic Skua, 9, 47–8, 57–9, 144, 193:
 clinal, 10, 47–8, 57–9; and female
 preference, 58; stability of, 10, 47–8,
 58, 144, 193, 261

- polymorphism (*cont.*)
 and assortative mating, 291
 of guppy, 190
 and heterozygous advantage, 236, 244,
 260;
 maintenance and stability of, 10, 218–22,
 223–5, 227–8, 229–31, 236, 243, 252,
 264, 267; by assortative mating, 243; by
 selection and migration, 10, 47–8, 58,
 261; by balance of selection pressure,
 48, 57, 58, 59, 269–70; by sexual and
 natural selection, 227–8, 229–31, 252,
 261, 268; by sexual selection, 144, 190,
 193, 218–22, 223–5, 233, 236
 protection of, 264, 267
 of ruff, 189
 unstable, 142–3, 268; and heterozygous
 disadvantage, 142, 268
- Pomarine Skua (*Stercorarius pomarinus*):
 evolutionary relationships with other
 skuas, 30; measurements of, 29;
 northerly distribution of, 30;
 phenotypic frequencies of, 30–1
- Popper, K.R., 172, 313
- population ecology, 264–5
- population genetics, 264, 267
- population numbers
 of Arctic Skua: in British Isles, 36;
 estimated, by counting, mapping or
 marking nests, 32–43; errors in
 estimates, 32, 34–5, 37; on Faeroe 37;
 on Fair Isle, 33, 41–3, 125, 265; in
 Finland, 37; on Foula, 34–6, 39–40,
 43–7, 125, 265; on Hermaness, 39,
 40–1, 125, 266; in Iceland, 33, 37, 52–5;
 on migration, 37; on Noss, 36, 40, 125,
 265, 266
- population regulation,
 in Arctic Skua, 45–6, 266
 density-dependent, 264, 266, 267
- preference, *see* female preference
- predation
 by Arctic Foxes on Arctic Skuas, 28
 by Arctic Skuas, 60
 by Bonxies on Arctic Skuas, 44–7, 92,
 173, 266, 277
 by Long-tailed Skuas, 30
- preferential mating
 of Arctic Skua, 89, 244–7; and breeding
 dates, 245
 assortative, 188, 238–43
 at equilibrium 218–22, 223–5, 251; with
 natural selection, 227–8, 229–31
 frequency-dependent advantage of, 192,
 211–2, 232, 268
 genetic models of, 215–31
 and ‘rare male’ effect, 190
- random mating combined with, 210, 211,
 214, 216, 240, 245–7, 250
- probability of survival, 120–1, 124; with
 constant death rate, 124
- Puffin (*Fregata arctica*), 37, 60–6, 115:
 Arctic Skuas’ attacks on 60–6; flight of,
 60–1
- Pygoscelis adeliae* (Adélie Penguin), 30
- quadrats, 183
- r*, *see* rate of increase, intrinsic
- R_o (net reproductive rate), 122–3, 130, 272,
 273, 274, 276, 279, 281
- RSPB, *see* Royal Society for Protection of
 Birds
- Raper, J.K., 211, 311, 313
- random mating
 in genetic models, 216, 217, 240; and
 fertility of, 217
 preferential mating combined with, 210,
 211, 214, 216, 240, 245–7, 250
- ‘rare male’ effect, 190, 212; in *Drosophila*,
 190; in guppy, 190; in preferential
 mating, 190, 212
- rates of increase
 of Arctic Skua: exponential, 42, 44, 121,
 125, 265; intrinsic, 121, 130, 139–42,
 267, 277–8, 281
 of bird populations, 271–84
 of Bonxies, 46, 266
 intrinsic, 45, 116, 121, 130, 139–42, 267,
 272–4, 277–8, 281
- Razorbill (*Alca torda*), 37, 60
- Red Grouse (*Lagopus lagopus scoticus*),
 164–5
- regression
 of breeding date and territory size,
 169–72, 176; hypothetical, 178
 of fledging period and breeding date,
 93–4
- of offspring and parents, 112–4, 117, 119:
 analysis of variance of, 115; and
 heritability, 112–4
- relative fitness (w), 123, 175, 206, 274
- reproductive rate
 age specific, 116, 121
 of Arctic Skua, 10, 127, 131, 133, 135–9,
 140, 277; and phenotypes, 133, 135–9,
 140
 natural selection of, 117
- reproductive success
 of Arctic Skua, 175–6
 and breeding date, 166, 173, 191
 of females, 191
 of males, 190, 191; variation in, 190, 191
- Richter-Dyn, N., 50, 269, 270, 311

Index

323

- ringing, of Arctic Skuas, 15–16, 198
 ringing recoveries, of Arctic Skuas, 48–9
 rings: lost by Arctic Skuas, 15, 197, 198;
 metal (BTO), 15; plastic, coloured, 16
 Rintoul, L.J., 40, 41, 309
 Robertson, Ian, 2
 Royal Society for Protection of Birds
 (RSPB), 40, 41
 Rudder, B., 190, 310
 ruff, 188, 189
 runaway process, of sexual selection, 174,
 185, 186, 188, 240
- s*, *see* selective coefficient
 Sandwich Tern, 60, 62, 63
 Saunders, D., 73, 310
 Seabird Group, 37
 Seiger, M.B., 239, 310
 selection, *see under*: apostatic selection;
 group selection; natural selection;
 sexual selection
 selective coefficient, *s*, 123, 142–4, 206–8,
 225, 274
 of Arctic Skua phenotypes, 142–4, 206–8,
 263, 267; and fixation of dark allele,
 142–4; sex differences in, 142, 267; of
 sexual selection, 206–8, 263
 semi-dominance, of Arctic Skua
 phenotypes, 19, 100, 216
 Semler, D.E., 188, 213, 313
 sex-limited characters, 187, 188–9, 229
 sexual behaviour, 9, 145–59
 of Arctic Skua: *Begging*, 156–7; the
 Begging Call, 156; copulation, 156–8;
 the *Copulation Call*, 156; divorce of,
 154–5, 156, 199; mating, 155–9; nest
 building, 158–9; the *Nest Call*, 158;
 pair formation, 152–3; of phenotypes,
 9; *Squeaking*, 157; the *Squeaking Call*,
 158; *Squeaking Scene*, 152, 158; the
 Willing Attitude of female, 156–8
 sexual dimorphism, 189, 190
 and polygyny, 189, 190
 sexual response, *see* female sexual response
 sexual selection
 of Arctic Skuas, 17, 89, 138–9, 142–4,
 179, 193–209, 247, 262–3; coefficients
 of, 206–8, 263; of males, not females,
 203; mechanism of, 262–3; test of,
 197–9
 balanced by natural selection, 184–5,
 188–9, 212, 225–31, 261, 263
 Darwin's theory of, 14, 166, 180–4
 frequency-dependent, 192, 212; and
 maintenance of polymorphism, 144,
 190, 193, 218–22, 223–5, 233, 236
 by male competition, 181, 182, 188, 208,
 232–8
 in monogamous species, 14, 152, 173,
 189–93, 210, 220, 222, 224, 227, 231–4
 in polygynous species, 189, 193, 211, 220,
 222, 224, 231–4
 runaway process of, 174, 185, 186, 188,
 240
 of territoriality, 73, 146, 164, 174–9;
 model of, 174–8
 sexual selective coefficients, 206–8, 263
 sexual selective values, *see* sexual selective
 coefficients
 Sheppard, P.M., 28, 309
 shooting, of Arctic Skuas on Fair Isle, 1, 18,
 42, 43, 127–31, 140, 155, 265
 Shetland, Arctic Skuas in, 1, 50, 52–8
 Snyder, G.A., 242, 311
 sociobiology, 46, 76, 181
 Southern Skua (*Catharacta skua*):
 evolutionary relationships with other
 skuas, 30; measurements of, 29
 Spitzbergen, Arctic Skuas in, 37, 50
 Southern, H.N., 10, 37, 50, 53, 56, 313
 Spiess, E.B., 190, 211, 310, 313
 Spiess, L.D., 190, 313
 spotted orchid (*Dactylorhiza fuchsii*), 8
 standard deviation, 111; of fledging period,
 93; of incubation period, 89
 Steele, R.G.D., 171, 313
Stercorariidae, 29–30
Stercorarius longicaudus, *see* Long-tailed
 Skua
Stercorarius parasiticus, *see* Arctic Skua
Stercorarius pomarinus, *see* Pomarine Skua
 stickleback, 188, 213, 229
 supernormal stimulus, 185, 187–8
 support, in units of log likelihood, 249, 250
 survival rate, of Arctic Skua, 10, 123–31,
 277; effects of shooting on, 127–31
- T*, *see* generation time
 Tanemura, M., 162, 311
 Taylor, I.R., 60, 61, 62, 63, 64, 313
 terns, 60–4: Arctic Skuas' attacks on, 60–4;
 flight of, 61
 territorial quality, 183
 territoriality
 and agonistic behaviour, 164
 of Arctic Skuas, 74, 76–9, 146, 173–9:
 and diet, 74, 76–9, 146, 173; for
 protection of chicks, 79, 173–4; sexual
 selection of, 73, 146, 164, 174–9
 of Herring Gull, 145
 territories
 of Arctic Skuas: change of, between
 years, 153–4; competition between

324 *Index*

- Arctic Skuas and Bonxies for, 9, 43–4, 160, 266; defence of, 6, 146–51, 160; as feeding areas, 74–80, 146; male tenure of, 154; mapping of, 18, 159, 162; phenotypic differences in, xv; polygonal, 161–3, 164; for protection of chicks, 79; size of, 73, 76, 160, 165, 169–72, 176–8
 - of mouthbrooder fish, 161, 162, of Pectoral Sandpiper, 162; and testosterone, 164–5, 179
 - territory size
 - of Arctic Skua, 73, 76, 160; and breeding date, 165, 169–72, 174–9; of phenotypes, 165, 166–9; and type of intruder, 160
 - and breeding season, 166
 - measurement of, 159–63: by fitting polygons, 162–3
 - optimum, 174
 - and testosterone levels, 164–5, 179
 - testosterone
 - and extended breeding season, 165
 - and territory size, 164–5, 179
 - Thearle, R.J.P., 25, 292, 312
 - threshold, of female response, 182, 210, 212, 214, 216, 250
 - Ticehurst, N.F., 17, 314
 - Tilapia mossambica* (mouthbrooder fish), 161
 - Torrie, J.H., 171, 313
 - Trillmich, F., 30, 313
 - Tucker, B.W., 17, 314
 - unstable equilibrium, 142
 - Uria aalge* (Guillemot), 37, 60, 78
- Valkenburg, P., 37, 310
- variance: of breeding dates, 201; bias in estimation of, 111; environmental, 111–2; formula for, 111; genetic, 111–2, 116, 117 (in fitness) 116, 117; in phenotypic expression, 112; *and see analysis of variance*
- variation
- continuous, 10, 19–20, 104, 110: of Arctic Skua phenotypes, 19–20, 104, 110; environmental and genetic factors of, 10, 110
 - in behaviour, 183–4: genetic, 183–4
 - in fitness, 116, 117, 190
- Voronoi polygons, of territories, 162–3, 164, 166
- w, see relative fitness*
- Walter, H., 307, 313
- Wandering Albatross (*Diomedea exulans*), 133
- Watson A., 164, 313, 314
- Wedd, N.S., 127, 313
- Westwood, N.J., 24, 25, 26, 292, 312
- Williamson, K., xiv, 10, 314
- Wilson, E.O., 72, 161, 314
- Witherby, H.F., 17, 115, 118, 156, 314
- Wynne-Edwards, V.C., 45, 46, 314
- Yates, F., 286, 314
- Yeates, G.K., 10, 314
- z* transformation, 171, 298