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Exploring mechanisms and origins of reduced dispersal in island Komodo dragons

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Loss of dispersal typifies island biotas, but the selective processes driving this phenomenon remain contentious. This is because selection via, both indirect (e.g. relaxed selection or island syndromes) and direct (e.g. natural selection or spatial sorting) processes may be involved, and no study has yet convincingly distinguished between these alternatives. Here, we combined observational and experimental analyses of an island lizard, the Komodo dragon (*Varanus komodoensis*, the world's largest lizard), to provide evidence for the actions of multiple processes that could contribute to island dispersal loss. In the Komodo dragon, concordant results from telemetry, simulations, experimental translocations, mark-recapture, and gene flow studies indicated that despite impressive physical and sensory capabilities for long-distance movement, Komodo dragons exhibited near complete dispersal restriction: individuals rarely moved beyond the valleys they were born/captured in. Importantly, lizard site-fidelity was insensitive to common agents of dispersal evolution (i.e. indices of risk for inbreeding, kin and intraspecific competition, and low habitat quality) that consequently reduced survival of resident individuals. We suggest that direct selection restricts movement capacity (e.g. via benefits of spatial philopatry and increased costs of dispersal) alongside use of dispersal-compensating traits (e.g. intraspecific niche partitioning) to constrain dispersal in island species.

1. Introduction

Astounding feats of long-distance dispersal often explain how animals colonize remote oceanic islands, a fundamental process in island biogeography [1–4]. However, it is the post-colonization dispersal tendencies of individuals, or alternatively their site fidelity, that strongly influences the evolutionary and ecological dynamics observed in island biota [5,6]. For instance, among Charles Darwin's most remarkable observations during his voyages were repeated accounts of flightless birds and beetles on islands [1,4]. Flightlessness is an extreme post-colonization phenotypic manifestation that inevitably leads to reduced dispersal ability in such organisms [7,8]. However, more than a century after Darwin, it remains unclear why restricted dispersal has evolved repeatedly in island

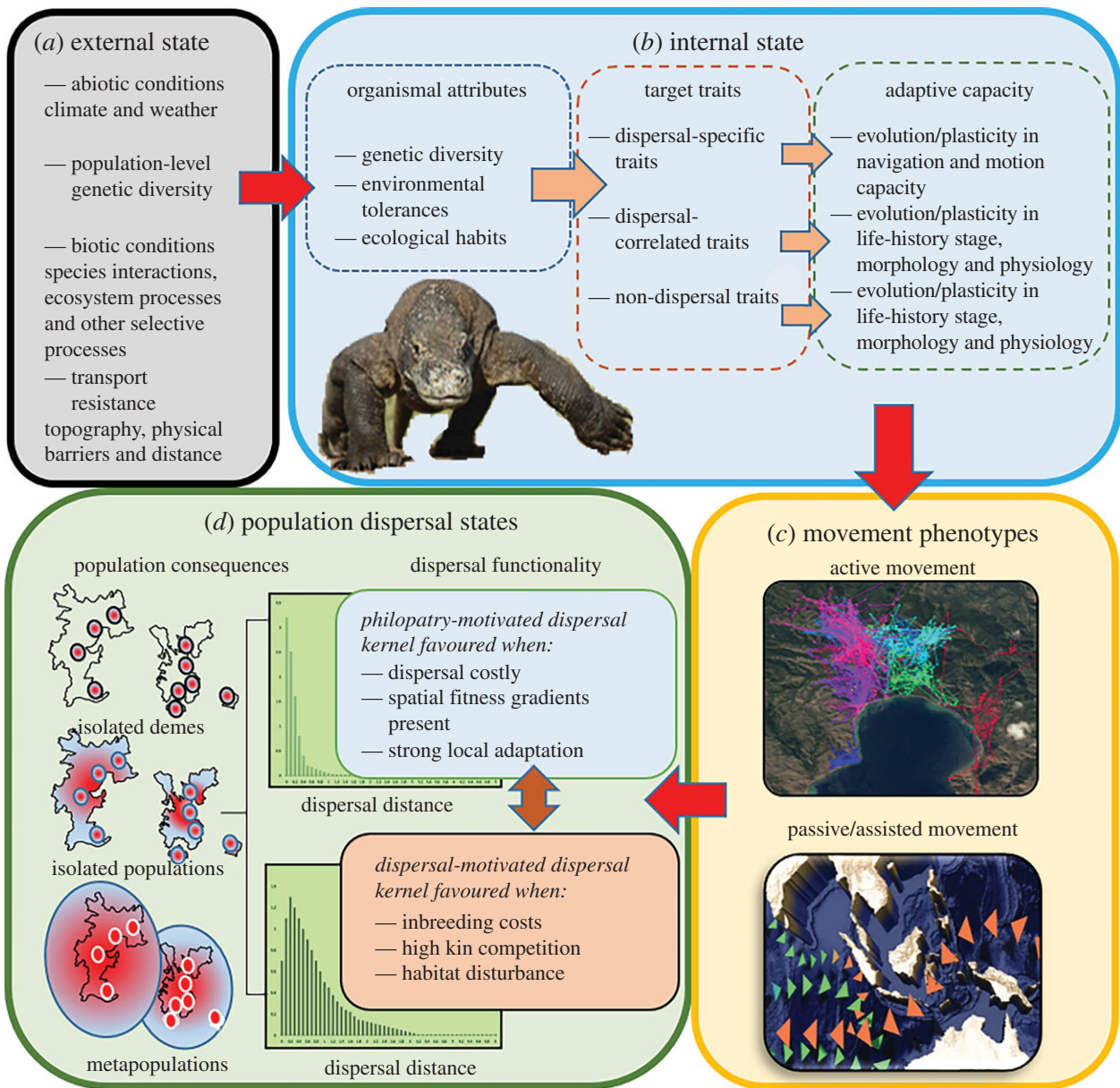


Figure 1. The conceptual model adapted from existing movement-dispersal frameworks [9,11,18] used to explain processes affecting the movement phenotype and dispersal state of island animals (e.g. Komodo dragons). This framework recognizes that multiple sources of multi-scale selection and counter-selection from abiotic and biotic processes, and population-level genetic diversity, could affect an individual's movement phenotype in time and space (a). Next, variation in an animal's movement phenotype is contingent on processes that affect plastic or evolutionary responses in navigation and motion capacities (b). Variation in movement phenotypes could also be indirectly affected by adaptive responses in other correlated or non-correlated traits (b). This framework also considers that passive or assisted ocean movements, due to actions of wind, waves, or currents, could also further influence movement phenotypes of island animals (c). Finally, the framework recognizes that aggregation of different individual movement phenotypes will constitute a population's dispersal state (d). A population's dispersal state as dictated by phenotypic movement variation across individuals can exist between the bounds of extreme site fidelity and extreme dispersal (d). (Online version in colour.)

organisms, particularly in species that have retained the capacity for dispersive movement.

Explaining the origins of variation in the dispersal abilities of animals be it on islands or continents is not simple [9–13]. As when exposed to a complex array of selective and non-selective processes, animals can use their organismal attributes and adaptive capacities to alter their movement phenotype, thus affecting a population's dispersal ability [11,14–17] (figure 1). In island animals at least five key processes could independently, or in combination, affect movement phenotypes to explain limited dispersal. First, animals that inhabit archipelagos are often exposed to strong spatial selection gradients that arise because environmental conditions can differ markedly between closely adjacent islands due to area- or elevation-related effects [6]. Spatial variation in environmental

or ecological conditions that result in fitness gradients can cause strong local adaptation (e.g. micro-evolutionary divergence) favouring selection for site fidelity and hence loss of demographic movement and gene flow [16,17,19,20].

Second, spatio-temporal variation in inbreeding, kin competition, or local habitat deterioration can present strong counter selection against philopatry, and promote phenotypic or evolutionary responses for increased dispersal [10,14,15]. However, if island animal dispersers have faced significant transition- (e.g. 'lost at sea') or colonization-related dispersal costs (i.e. proved to be maladapted to a different island environment), then genes for low dispersal in the remaining population will be prevalent, and result in philatropic individuals [17,19]. Importantly, if such events have occurred historically and led to severe dispersal loss, without

subsequent mutation or random gene-flow events restoring adaptive movement variation, negligible dispersal may remain irrespective of contemporary selection [16,17,19,20].

Third, indirect selection is another island-centric process that could reduce the movement and dispersal tendencies of animals in archipelagos [21–23]. An often cited example of this phenomenon is that of birds colonizing Pacific islands and incurring relaxed predation pressure, eliminating the necessity for escape through flight [8,22]. Consequent accumulated neutral mutations led to the evolution of vestigial flight structures (i.e. flightlessness) that indirectly reduced movement and dispersal abilities [21]. More broadly, indirect selection could affect dispersal whenever individuals confined to unique island environments evolve substantial differences in morphology, life history, and behaviour relative to continents. For example, island animals show conspicuous evolution in body size, or develop island syndromes, as a response to natural or sexual selection [24]. These broad scale phenotypic changes can indirectly affect locomotor systems, bodily reserves, physiological tolerances, or life history, all qualities that influence movement and dispersal abilities of island animals [9,18].

Fourth, although all aforementioned mechanisms affect movement phenotypes that physically govern dispersal variation in island animals; theory recognizes that organisms can filter selection, so that non-movement-related traits could instead resolve an individual's fitness. For instance, inbreeding avoidance often favours increased dispersal among individuals at small spatial scales [10,14,15]. However, selection for dispersal may be negligible if, instead, individuals avoid the costs of inbreeding by using kin recognition or promiscuous mating habits that achieve better fitness outcomes [25].

Fifth, many terrestrial animals can potentially swim, float, or raft between insular populations [1–3,5]. Indeed, such movements partially or fully assisted by the actions of wind, waves, tides, or ocean currents are known to have major ecological and evolutionary implications for island populations [5,26–29]. Nevertheless, the role of environmental determinants on terrestrial animal movement and gene flow is again complex, as successful ocean dispersal can require strong coupling between an animal's traits and favourable transport conditions.

In this study, we consider evidence for multi-causality to explain how reduced dispersal an often cited 'island-centric' dispersal state [1,4] arises in island animals, using the world's largest lizard, the Komodo dragon (*Varanus komodoensis*) as a case study. Although this species, like many other island endemics, retains good physical movement capabilities, they nevertheless exhibit strong patterns of genetic differentiation among island populations suggesting a basis for restricted dispersal [30]. However, the putative processes, and ensuing phenotypic mechanisms, that could produce a restricted dispersal state remain unknown. To address this objective we used a combination of seven types of individual movement and population-level dispersal data measured from Komodo dragons across 10 sites located on four islands in Komodo National Park in eastern Indonesia over 10 years of research. If, as predicted, Komodo dragons exhibit limited dispersal then we would expect to observe movement phenotypes constrained by physical or behavioural attributes that limit longer distance dispersal movements or gene flow between, and even within, island populations. Finally, in recognition that reduced dispersal could arise from the actions of multiple processes we consider and discuss the relative evidence for their respective actions. For example, reduced

dispersal arising from selection for the benefits of philopatry, or the costs of dispersal, could be expected to be more prevalent at large spatial scales (e.g. due to spatial fitness gradients, or transport or settlement costs of dispersal between islands). In contrast, at smaller spatial scales (e.g. within islands), the use of alternative non-dispersal-related mechanisms could be necessary to avoid fitness loss due to kin competition and inbreeding often offset by increased dispersal at this scale.

2. Material and methods

(a) Study system

Our study was conducted in Komodo National Park (8°35'22" S, 119°36'52" E) in eastern Indonesia (electronic supplementary material, figure S1). Here, we used 10 sites spread over the four islands that retain Komodo dragon populations. Four sites were located on Komodo Island: (i) Loh Liang (K1), (ii) Loh Lawi (K2), (iii) Loh Sebita (K3), and (iv) Loh Wau (K4). Another four sites were located on Rinca Island: (v) Loh Buaya (R1), (vi) Loh Baru (R2), (vii) Loh Tongker (R3), and (viii) Loh Dasami (R4). A single site was located on each of the two small islands: (ix) Gili Motang (hereinafter 'Motang') and (x) Nusa Kode ('Kode') (electronic supplementary material, figure S1). All sites were similar with respect to elevation and comprised open deciduous monsoon forest interspersed with woodland or savannah grassland (electronic supplementary material, figure S2).

It was at these 10 sites that biotelemetry, translocation, mark-recapture, and population genetic studies were performed. However, two additional sites (the Wae Wuul Nature Reserve (WW; 14.2 km²), located on Flores Island and Padar Island) within Komodo National Park were used in biotelemetry and translocation studies of Komodo dragons, respectively (electronic supplementary material, figure S1).

(b) Telemetry

We used telemetry to ascertain information on Komodo dragon movement behaviour for two purposes: first, to ascertain body-size-related variation in Komodo dragon daily movements to gauge capacity for movement across ontogeny; second, to identify exploratory movement behaviour beyond typical movements within home range areas. To evaluate body-size-related differences in daily movement rates, we first attached very high frequency (VHF) and the Global Positioning System (GPS) transmitters to 22 Komodo dragons ranging from hatchlings through to the largest males in the K1 site on Komodo Island. We monitored dragons for a mean (\pm s.e.m.) period of 151.7 ± 31.9 days. Movement data were collected automatically (GPS collars, Televilt, Sweden) or manually (VHF collars, AVM Instruments, USA), the latter by using Yagi antennas and VHF receivers (AVM) to visually locate dragons. We collected five fixes per dragon per day at approximately 3 h intervals between 06.00 and 18.00 in order to estimate daily movement rate. We used a general additive mixed model (GAMM) implemented in the program R to evaluate the relationship between daily movement (i.e. defined as total path distance travelled per day estimated from the addition of four daily step length distances) and dragon body mass. Dragon ID was used as a random effect in the model.

Next, we defined the exploration ability of Komodo dragons as their capacity to undertake brief long-distance movements (i.e. greater than 1 day but less than 7 days) that took individuals beyond their home ranges. To determine exploration ability, we combined radio-tracking data collected from the K1 site with data from two similar studies employing similar sampling methods [31,32]. These studies provided additional VHF radio-tracking data from 33 dragons at three additional sites: two in Komodo National Park (K3, R1) and one in Wae Wuul Nature Reserve

(WW) on Flores Island [31,32]. In combination, the telemetry dataset comprised 55 dragons sampled for 4115 independent telemetry movements (defined as the linear distance between two telemetry fixes), from which we measured exploratory behaviour (defined as a dragon's capacity to undertake various degrees of movement beyond its resident valley). We categorized all individual movements into intra-valley (movement confined to resident valley), inter-valley (movement into another valley), and inter-island movements (dragons swimming to neighbouring islands). Given the absence of exploratory behaviour outside of intra-valley movements, we reported the results without statistical analysis.

(c) Simulations of daily displacement for understanding movement behaviour

To further evaluate the relationship between movement behaviour and dispersal capacity in Komodo dragons, we compared daily displacement (i.e. defined as the distance between the starting location and the last location within a day) with those simulated using a simple random walk. For 22 Komodo dragons, we calculated daily displacement distances from aforementioned telemetry data. We then used a simple random walk model that resampled (at random) 10 000 daily displacement distances from each individual to produce a simulated estimate of daily displacement following published methods [33]. We then used these simple random walk-based displacement distances in order to compare the observed daily displacement to what the dragons could have done if they just moved at random.

(d) Translocations

On three separate occasions over the duration of our study, Komodo National Park staff (assisted by this study's authors) undertook one inter-island and two intra-island translocations with a total of seven adult male Komodo dragons (i.e. lizards greater than 35 kg mass). The translocations proved especially useful for examining the physical, navigational, and homing attributes of Komodo dragons would be necessary for undertaking long-distance dispersal or homing-type movements within and between islands. During October 2007, two adult male Komodo dragons were captured near Komodo village (8°35'19.80" S, 119°29'32.81" E) on Komodo Island, restrained (using tape and rope) and transported by boat to intra-island locations 5 and 8 km from their capture point. During February and March 2013, two adult male dragons were translocated and released at two intra-island locations at 15 and 22 km from their capture points at the Loh Buaya ranger station (located within the R1 site) on Rinca Island. In 2014, three adult dragons were again taken from Loh Buaya ranger station and Rinca village (8°37'14.39" S, 119°47'5.88" E) on Rinca Island, then translocated and released onto Padar Island. Padar is the third largest island in Komodo National Park and currently does not support a Komodo dragon population. For dragons translocated and released onto Padar Island, the shortest over water path distance for return to Rinca Island was 2.1 km.

To determine Komodo dragon movement outcomes (i.e. returned successfully or failed to return), we relied on direct observations from park rangers who were stationed permanently at the departure and arrival locations. All dragons were painted with large coloured markings (using non-toxic oil-based paint) across their backs, so that they would remain identifiable for up to 2 years after release.

(e) Capture–mark–recapture field methods

From 2003 to 2012, we conducted annual capture–mark–recapture fieldwork during the dry season (March–November) at 203 fixed trapping locations at the 10 sites spread over the four islands in Komodo National Park. Within each study site during each year, baited cage traps [24] (electronic supplementary

material, figure S3) for capturing Komodo dragons were placed at individual trapping locations (K1 = 32, K2 = 32, K3 = 21, K4 = 9; R1 = 22, R2 = 22, R3 = 13, R4 = 24; Motang = 16; Kode = 12) (electronic supplementary material, figures S4 and S5). The number of trapping locations was commensurate with the area and vegetation structure of each study site. Additionally, to capture hatchlings prior to them becoming arboreal (and more difficult to capture), we fenced active Komodo dragon nests with aluminium sheeting and covered these enclosures with netting to prevent escape. During February and March, nests were monitored daily for emergence of hatchlings. On emergence, all hatchlings were collected and processed using protocols described below.

Following capture, each dragon was permanently identified using a passive integrated transponder (Microchips Australia Pty Ltd, Australia) inserted subdermally into the right hind leg. We extracted 0.1 ml of blood from each lizard's caudal vein (using a 3 ml syringe and 23G × 2.54 cm needle) and then preserved the sample in a 2.0 ml cryotube containing lysis buffer (0.1 M Tris buffer, 0.1 M EDTA, 0.2 M NaCl, 1% sodium dodecyl sulphate, pH 8.0) until subsequent genetic analysis. Komodo dragons were released at their point of capture within approximately 15 min of being removed from the trap. A summary of lizard captures, including site-specific sample sizes, recapture statistics, and the age- and size-based composition of marked Komodo dragons, is presented in electronic supplementary material, table S1 and table S2, respectively.

(f) Methods for estimating dispersal model covariates

We used multi-state mark–recapture models [34] to consider how site-specific and individual-based covariates concurrently influenced variation in Komodo dragon survival and dispersal rates, respectively. These processes are briefly described below (and the site-specific mean (\pm s.e.m.) values for each site-level estimate are presented in electronic supplementary material, table S3):

- (1) *Ungulate prey biomass density*. Spatial variation among and within islands in biomass densities (i.e. kg prey/km²) of Rusa deer (*Rusa timorensis*), wild pigs (*Sus scrofa*), and water buffalo (*Bubalus bubalis*) could influence the dispersal and survival of Komodo dragons. We used faecal counts, corrected based on their relationship with animal density and biomass, to estimate site-specific ungulate biomass [35,36].
- (2) *Komodo dragon inbreeding coefficients and relatedness*. To estimate site-specific inbreeding coefficients and relatedness values, we genotyped 248 Komodo dragons (captured within this study) at 16 species-specific nuclear DNA microsatellite loci [37,38]. We used Monte Carlo simulations implemented in the program COANCESTRY (v. 1.0.1.2) to identify the most appropriate inbreeding coefficient and relatedness estimates for our data [39].
- (3) *Komodo dragon density*. Survival and dispersal rates of vertebrates can be strongly influenced by density-dependent processes [10,40]. To enable evaluation of density-dependent effects on Komodo dragon survival and dispersal, we estimated site-specific densities using the Jolly–Seber (JS) method in the program MARK [41], following protocols outlined elsewhere.
- (4) *Habitat quality*. Biophysical factors could also influence the survival and dispersal rate of island endemics [42]. We therefore estimated a broad scale and composite habitat quality index for each site. This index included five variables (prey biomass, vegetation composition, water course length, island area, and site isolation). We combined these five measures into a single composite index of environmental site quality, using a principal component analysis [43]. Our habitat quality index was the factor score from the first axis of the principal component analysis.
- (5) *Geographical distance*. The probability of organismal dispersal movements commonly decay with distance (i.e. a dispersal

kernel) [44]. Hence, the dispersal frequency of Komodo dragons was expected to decrease as geographical distances (e.g. between sites) increased [8,15].

- (6) *Terrain*. Landscape resistance, affecting movements, is likely to vary with the terrain that individuals move across. For highly terrestrial species such as Komodo dragons, which are rarely observed to swim, we would expect more frequent and longer movements to occur on land than across bodies of ocean separating islands [24].
- (7) *Body size*. Phenotypic traits such as body size can be associated with an individual's propensity to disperse [20]. We considered the effect of mean snout to vent length (SVL) on the probability of an individual dispersing.
- (8) *Body condition*. An individual's body condition can strongly influence dispersal ability [11]. We used the residual from the linear relationship between the logs of mass (kg) and SVL as an index of Komodo dragon body condition.

(g) Incidental observations of open-water dispersal

While our study design was aimed at measuring direct dispersal and gene flow between the 10 study sites on the four islands that harbour Komodo dragon populations, we recognized that our ability to measure important dispersal events, such as individuals colonizing one of the many uninhabited islands within Komodo National Park, was negligible. As a result, to aid our understanding of the open-water dispersal ability of this species, for sightings of Komodo dragons on the smaller uninhabited islands, we relied on anecdotal observations drawn from 10 years of regular and wide-ranging ranger patrols.

(h) Estimation of annual displacement for understanding dispersal behaviour

We calculated annual displacement (i.e. defined as the distance between an individual's first point of capture and recapture localities in subsequent years) for Komodo dragons using capture–mark–recapture data. Annual displacement distances were estimated for 1115 marked individuals across 2097 captures compiled during fieldwork between 2003 and 2012. A probability distribution was then calculated to present annual displacements observed in Komodo dragons.

(i) Demographic movement analyses

Multi-state models in the program MARK were used to quantify Komodo dragon site-to-site dispersal and survival [34,40]. Multi-state models simultaneously estimate apparent survival (Φ), resighting (P), and dispersal (ψ ; or site fidelity as $1 - \psi$) between sites [41]. A candidate set of 33 models was assessed to evaluate survival and dispersal estimates in Komodo dragons. These models considered variation in parameter combinations influencing Φ and ψ . To simultaneously model site variation in dispersal and survival probability as a function of covariates that might be relevant to Komodo dragons, we constrained both Φ and ψ to be fitted with various combinations of the five site-specific covariates (i.e. prey biomass, inbreeding coefficients, relatedness estimates, dragon population density, and habitat quality) and modelled the recapture parameter as group-specific (i.e. a function of the site) or constant (.). To accommodate the possibility of interactive effects of these covariates on dispersal and survival, we fitted some models with additive (+) and others with multiplicative (*) covariate combinations. We also considered several non-covariate models (e.g. null and fully time- and group-dependent models) to enable assessment of models fitted with covariates; here, the survival, capture probability and dispersal parameters were fitted with combinations of time (t), group (g , i.e. site) or constant terms. Multi-state models were ranked using the quasi-likelihood Akaike

information criterion corrected for small sample-size (AIC_c) value (QAIC_c) to account for overdispersion. Individual model weights (w_i), a measure of relative support for a model, were estimated [45]. We used UCARE to assess goodness-of-fit and estimate \hat{c} (the overdispersion parameter) [46]. Results were adjusted for overdispersion in the program MARK using QAIC_c based on a \hat{c} value of 1.7. We present site-specific model parameter estimates for survival and site fidelity, using the top-ranked model because it had substantial support (i.e. model weight = 0.75) among candidate models. Key assumptions of the multi-strata models—(i) equal capture probabilities among individuals within a population, (ii) capture occasions are non-lethal and instantaneous events, and (iii) emigration is permanent—were not strongly violated in our study ([42]; electronic supplementary material, appendix 1).

(j) Estimates of recent gene flow

Rates of recent gene flow (i.e. past 1–3 generations, i.e. approx. 8–24 years) between sites were assessed using a Bayesian Markov Chain Monte Carlo (MCMC) multi-locus approach implemented in BayesAss [47]. Here again, we used the aforementioned 248 Komodo dragons genotyped at 16 species-specific nuclear DNA microsatellite loci across our 10 field sites. The MCMC was run for 3×10^7 iterations and sampled every 2000, and the first 1×10^6 iterations were discarded as burn-in iterations. Estimates of migration (mean and 95% credible intervals) were obtained from the posterior distribution. Mantel tests (10 000 iterations) were used to evaluate relationships between gene flow, geographical distance, and the effect of the terrain [land (intra-island) and ocean (inter-island)] between sites.

3. Results

(a) Individual movement behaviour

Komodo dragon movements derived from telemetry data ($n = 22$ individuals tracked for 151.7 ± 31.9 days, 5 fixes/day) indicated that body size produced a significant curvilinear relationship in daily dragon movement distances (GAMM, $F = 6.69$, $n = 2921$, $p < 0.001$). Here, it was evident that dragons between 16 and 22 kg moved most, with some individuals averaging a total daily movement distance (i.e. sum of four daily step length measurements) of approximately 2.5 km per day. However, because of extensive variation in daily movements, individuals could travel as far as 11 km per day, and often over steep terrain (figure 2a). Further use of VHF telemetry at additional sites ($n = 55$ dragons; 4115 independent movements) confirmed that home ranges of individuals were restricted entirely to their local valley; exploratory terrestrial movements (between valleys) or aquatic movements (between islands) were never recorded (figure 2b). Telemetry therefore revealed that dragons had substantial capacity for movement within sites, moving considerable distances through a range of habitats and terrain, but not outside these areas.

To further evaluate how Komodo dragon movement behaviour contributed to apparent site fidelity, despite good mobility, we compared observed daily displacement distances against those simulated from a simple random walk model. Observed daily dragon displacements were significantly shorter than those estimated using this model (figure 2c). This result reflected that Komodo dragon movement behaviour, via limited daily displacement, strongly reinforced spatial fidelity.

While Komodo dragons did not move beyond their local valley, we found that they nevertheless possessed remarkable navigational and homing capability. We experimentally

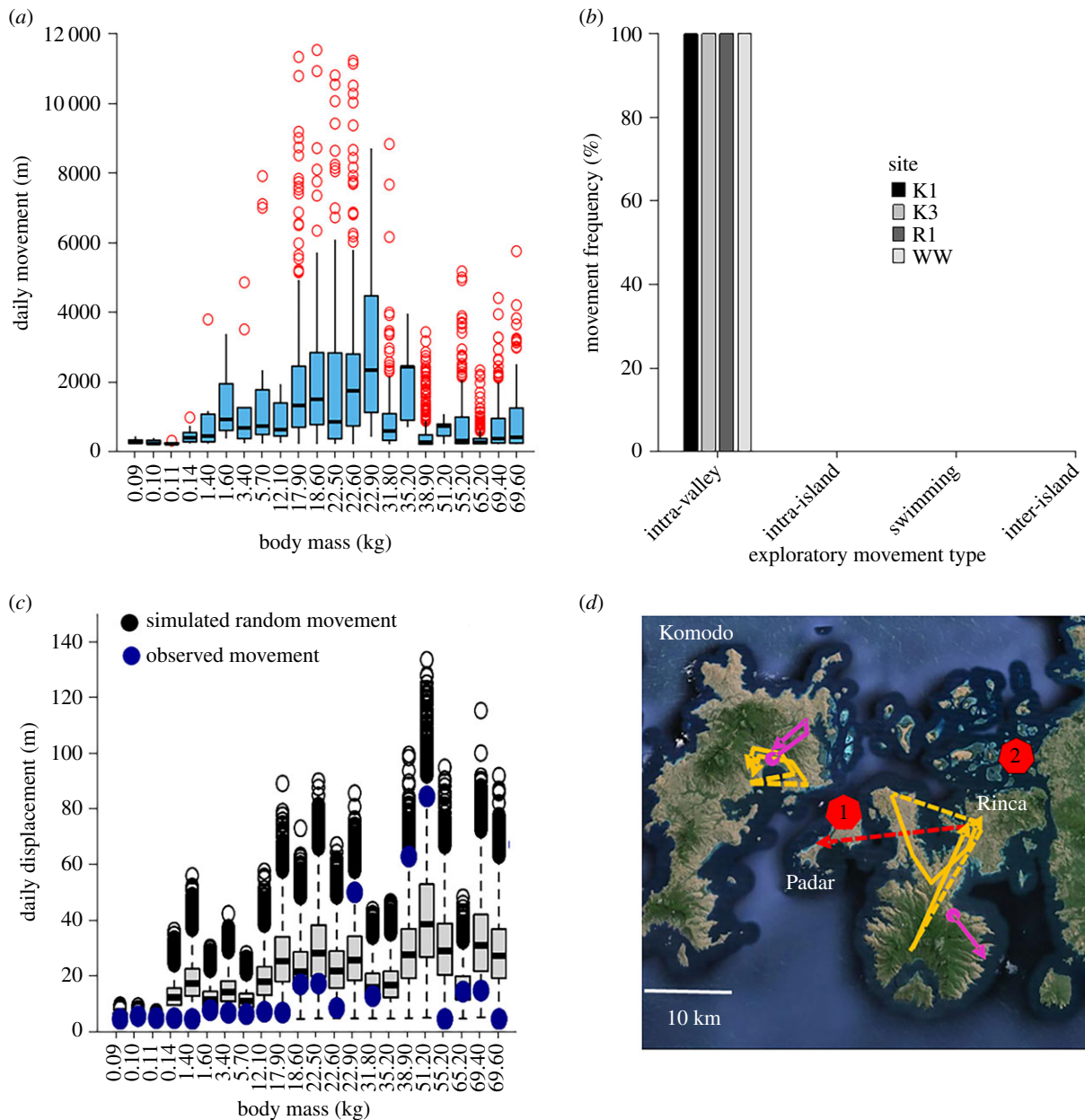


Figure 2. Characteristics of Komodo dragon movement in Komodo National Park. (a) Total daily movement distances of Komodo dragons as a function of body mass. (b) Frequency of exploratory movement types observed in Komodo dragons at four sites. (c) Comparison of observed and simulated random walk daily movements for Komodo dragons as a function of body size. (d) Satellite imagery of the study area depicting Komodo dragon path movements from natural intra-island (pink arrows) and inter-island movement (hexagons) events and intra-island (yellow arrows) and inter-island (red arrow) experimental translocations.

translocated four individuals within islands, releasing them up to 30 km from their original capture site. All returned to their original capture locations within four months (range 4–131 days). However, translocations of individuals from Rinca to Padar islands ($n = 3$) did not prompt similar homing, and more than 3 years after translocation, all individuals remained resident (figure 2d).

(b) Population-level dispersal and gene flow

Ten years of mark–recapture study of hatchling, sub-adult, and adult dragons ($n = 1115$ marked individuals; approximately 45% of the total population) was used to estimate the frequency of dispersal between 10 sites distributed across four islands in Komodo National Park (electronic supplementary material, figure S1). The distribution probability of observed annual displacements (median distance of $272.6 \pm$

20.9 m from first capture) clearly indicated that, even over a decade, Komodo dragons remained highly site faithful and had an extremely limited capacity for long-distance dispersal (figure 3a).

Next, using multi-state models, we modelled survival (Φ) and dispersal (Ψ) in relation to widely demonstrated determinants of survival and dispersal rates in vertebrates; ungulate prey biomass (a proxy for food availability), genetic relatedness, inbreeding coefficients, population density, habitat quality, geographical distance, and phenotypic traits. The best model (model weight (w) = 0.75 (electronic supplementary material, table S4)) included an additive effect of prey biomass and population relatedness on dragon survival rate (Φ). Despite the strong effects of these covariates on survival, the corresponding dispersal rate (Ψ) was invariant and negligible (approx. 0.01%), with 99.99% of movements resulting in site fidelity to resident valleys (electronic supplementary

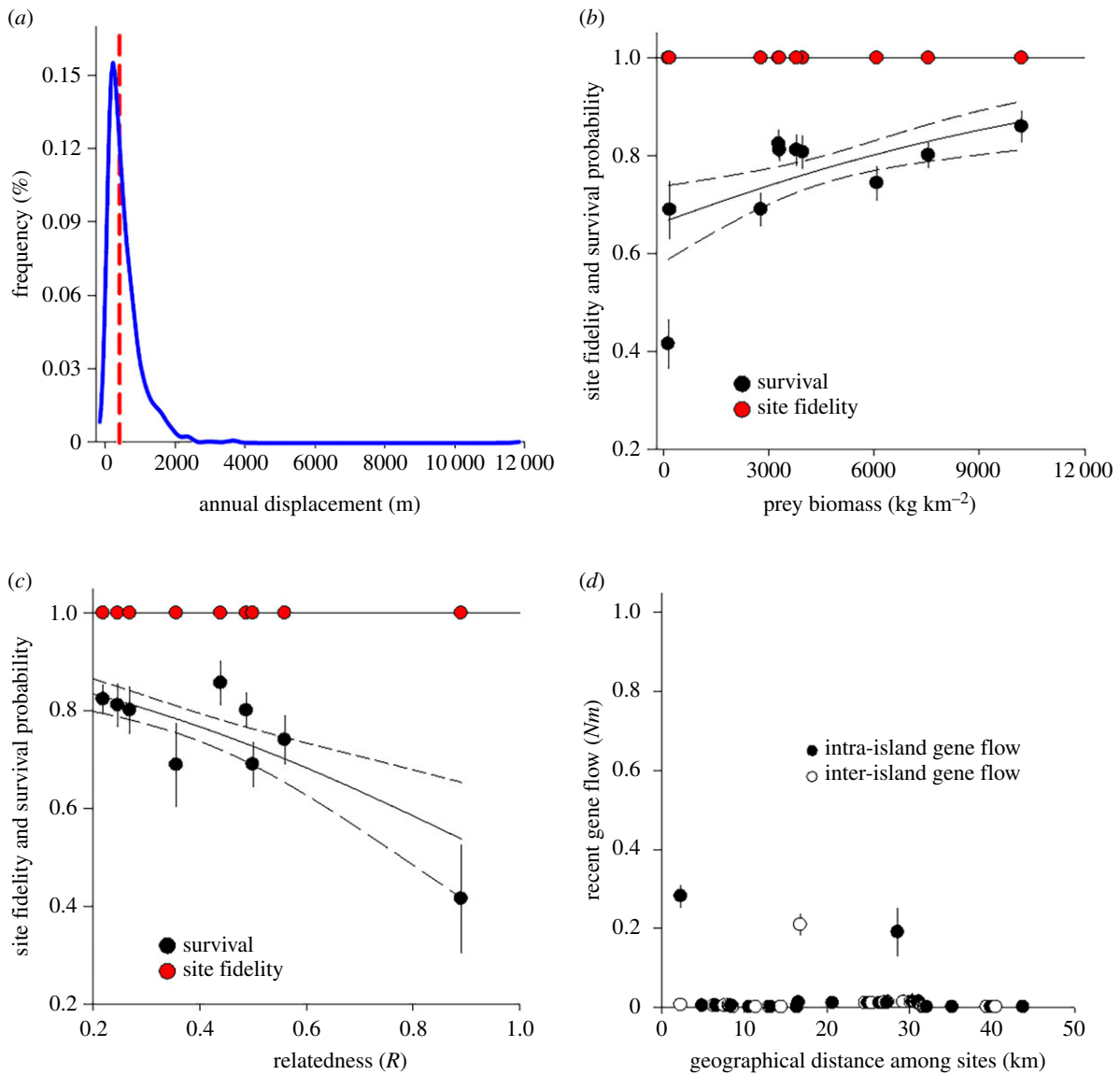


Figure 3. Characteristics of Komodo dragon dispersal in Komodo National Park. (a) The probability distribution of observed annual displacements (red dashed line is median distance) for Komodo dragons derived from mark-recapture data. Mean site fidelity ($\pm 95\%$ confidence intervals) and survival ($\pm 95\%$ confidence intervals) probabilities of Komodo dragons in relation to site differences in ungulate prey biomass (b) and genetic relatedness (c). (d) Recent Komodo dragon gene flow, estimated as migrants per generation ($Nm \pm 95\%$ credible intervals), as a function of distance and terrain between the 10 study sites. Intra-island and inter-island gene flow indicate dispersal across land and sea, respectively.

material, table S4; figure 3*b,c*). Remarkably, dispersal was unresponsive to key selective agents reducing survival, suggesting that selection against dispersal must be intense, ongoing, and sufficiently strong to negate the survival benefits of dispersal. Additional models were used to test the effects of extensive variation in body size or body condition, but again there was a negligible effect of these traits (which are synonymous with influence over animal dispersal capacity) on Komodo dragon movements. In effect, only 0.2% of individuals (2 of 1098; $n = 2097$ recaptures) dispersed between sites, and none between islands (figure 2*b*). None of our marked hatchlings ($n = 130$) recaptured as immature lizards ($n = 5$) had undertaken dispersal movements outside their natal valley, consistent with strong natal philopatry.

Estimates of recent gene flow (less than two generations), using microsatellite data from each of the 10 study sites, suggested rates of gene flow were very low, with the estimated number of migrants per approximately 8 year generation (N_m) ranging from 0.001 [0–0.015, 95% credible interval (CI)] to 0.269 (0.216–0.323, 95% CI) across pair-wise site combinations

(figure 3*d*). Neither geographical distance (Mantel test: $Z = 15.01$, $r = -0.02$, $p = 0.45$) nor terrain type (ocean versus land; partial Mantel test: $Z = 11.07$, $r = -0.01$, $p = 0.75$) influenced rates of recent gene flow.

Finally, 10 years of intensive ranger patrols on the islands resulted in only two reports of transoceanic crossings by dragons onto smaller islands uninhabited by conspecifics (figure 2*d*). Dispersal via ocean movement, although important for some island lizard species, is extremely rare in Komodo dragons.

4. Discussion

Theoretical and empirical studies increasingly recognize that multi-causality underpins variation in individual movement phenotypes contributing to a population's dispersal ability (and thus meta-population functionality) at various spatial and temporal scales [11,14–17]. Our study of Komodo dragons revealed that they retain impressive physical movement and homing capacity, yet exhibit stringent site fidelity and remain

confined almost exclusively to their resident valleys. Similarly, despite close proximity and strong currents among islands, ocean dispersal was extremely rare. Extreme philopatry occurs in Komodo dragons despite evidence for spatio-temporal variation in genetic (e.g. high inbreeding estimates), environmental (e.g. decreasing prey availability), and demographic factors (e.g. population declines on small islands [48]), attributes known to increase dispersal ability in other species [16,26]. Importantly, the dispersal state of Komodo dragons contrasts strongly with many of its congeners, including the Australian Lace Monitor (*Varanus varius*; i.e. the closest relative) and the semi-aquatic Asian water monitor (*Varanus salvator*; i.e. sympatric relative), which although much smaller in body size and having less movement capacity, have shown extremely high historical and contemporary dispersal across eastern Australia and South East Asia, respectively [49,50].

The phenotypic basis to restricted dispersal in Komodo dragon clearly does not arise from any 'classic' loss of physical traits (e.g. flightless island birds or beetles, [22,51]) that limit movement. As telemetry data indicated that Komodo dragons possess impressive physical movement capabilities allowing for extensive daily movement over difficult terrain. Excellent movement capacity is consistent with this lizard's foraging ecology that involves the hunting of large, active, and highly dispersed ungulate prey [52]. However, results of experimental translocations and simulations indicate that Komodo dragons apply avoidance and homing behaviour to restrict movement-related displacement. Most telling was that the Komodo dragons subjected to inter-island translocations remained resident 3 years after settlement onto a novel island. This fidelity suggests lizards avoid ocean crossings to return to resident islands. Similar behaviour is reported for volant tropical birds (on islands or in rainforests), that despite good flight capacity, are reluctant to cross narrow habitat barriers (e.g. ocean, rivers, or pasture) [53,54]. Thus Komodo dragons could be considered 'psychologically constrained' as behaviour restricts dispersal across even the narrowest of water crossings (approx. 1 km) that separate habitable islands. In contrast, those lizards subject to long-distance intra-island translocation (7–30 km) all demonstrated excellent homing behaviour as they successfully navigated return to resident valleys. These results suggest that like other reptiles, Komodo dragons have excellent navigational and sensory abilities to facilitate homing behaviour [55]. Thus pending context, Komodo dragons through behaviour can constrain movements or reinforce site fidelity to effectively limit dispersal.

We suggest that multiple processes occurring at different spatial scales could produce a strong phenotypic basis to reduced dispersal in Komodo dragons. Limited lizard dispersal among island populations, could arise in response to both the benefits of philopatry and the costs of dispersal. Here, we suggest that substantial environmental differences between closely adjacent islands presents Komodo dragons with long-running spatial selection (i.e. island-specific fitness landscapes) favouring reduced dispersal. Spatially mediated selection often favours local adaptation that increases spatial philopatry [16,56]. Over generations, increasing benefits of local adaptation would promote heightened site fidelity [12,14,57]. Here, locally adapted individuals gain higher fitness compared to individuals who have moved elsewhere (i.e. down a fitness gradient), even if, in the unlikely event, such individuals do not incur dispersal costs [20]. Evidence for a strong spatial fitness gradient favouring philopatry restricting dispersal is provided

by the fourfold difference in Komodo dragon body mass between island populations [24]. These large body size differences suggest that variation in island-specific prey biomass provides a basis to strong local adaptation among island populations that would act to benefit philopatry and increase costs of dispersal among island populations [58].

It is more perplexing that a similar pattern of restricted movement and gene flow also occurred within island populations. As within island populations, individuals would be expected to be exposed to weaker selection from spatial fitness gradients and movement-related transport or colonization costs, thus making dispersal-related fitness gains possible—especially if the costs of kin-related or density-dependent competition or inbreeding favoured increased dispersal by individuals at this scale [11,18]. Nevertheless, the observed negligible rate of Komodo dragon dispersal within island populations could arise for several reasons. First, philopatry at smaller spatial scales may persist if, via co-adapted gene complexes, learning, or experience, Komodo dragons maintain higher survival or reproduction by utilization and knowledge of local environmental conditions including prey, nesting localities, or avoidance of predators (e.g. conspecifics) [14,59]. Second, costs of dispersal may also exist at smaller scales if intraspecific aggression or cannibalism [59] increase for individuals that move beyond their home range into socially unfamiliar habitat. Similarly, dispersal is not the only way in which animals diminish fitness costs from competition or inbreeding. For example, niche partitioning is an extremely effective means by which animals reduce fitness costs arising from intraspecific competition that might otherwise increase dispersal [60]. Komodo dragons demonstrate extensive ontogenetic niche partitioning in dietary and habitat resources, a consequence of extreme body size variation across an individual's lifespan [52]. Effective resource partitioning among Komodo dragons could relax density-mediated competition, benefit philopatry, and reduce selection for dispersal. Similarly, heightened kin recognition and promiscuous mating systems (common to reptiles) can reduce the risk of inbreeding in other dispersal-limited species [25]. Alternatively, dispersal loss observed between island populations could mean that Komodo dragons have evolved canalization for extreme site fidelity at all spatial scales (i.e. a range-wide effect). This idea of canalization of dispersal loss is untestable, but given the surprising concordance in movement- and dispersal-related evidence it could have been achieved in Komodo dragons [16,17,19,20].

What can we infer from the rare longer distance and inter-population dispersal events made by Komodo dragons? These events comprised two inter-island movements and one moderate pair-wise estimate of gene flow (i.e. $Nm \sim 0.3$, which equates to 1 migrant dispersal event every approximately 24 years). We do not know the motivation for these events, but if it was similar to that for long-distance dispersal reported in other animals, then they are likely to have been stochastic and current-assisted, rather than informed active movements [4,61]. In other island reptiles, open-water dispersal events attest to the well-recognized benefits of long-distance dispersal—scope for genetic connectivity, the colonization of vacant islands, and the persistence of otherwise largely isolated island populations [4,61,62]. For example, some small island reptiles possess good tolerances to salt-water exposure, starvation, and dehydration and, when aided by favourable currents, can achieve significant rates of ocean-mediated dispersal [2,5,28]. However, for many other species, unsuccessful

passive dispersal is likely simply because storms are infrequent, the direction and duration of transport is unfavourable, or -dispersers suffer prolific fitness loss on colonization. For Komodo dragons, however, it remains unknown to what extent these rare over-water dispersal events influence either a disperser's fitness, or in the single example of inter-population gene flow, the ecological or evolutionary dynamics of recipient populations [61].

Komodo dragons suggest how complex processes can enable restricted dispersal in island animals [1,6,54]. Nevertheless, a limitation of this study is that we were unable to determine which, of potentially multiple, processes caused limited dispersal in Komodo dragons. To do so we must now undertake manipulative experiments (e.g. using reciprocal transplant or common garden experiments) [58], complemented with comparative approaches [63], to quantify how different ecological and evolutionary processes causatively explain restricted dispersal in Komodo dragons [18].

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