Polyandry in a marine turtle: Females make the best of a bad job

Patricia L. M. Lee* and Graeme C. Hays

School of Biological Sciences, Institute of Environmental Sustainability, University of Wales Swansea, Swansea SA2 8PP, United Kingdom

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The female perspective on reproductive strategies remains one of the most active areas of debate in biology. Even though a single mating is often sufficient to satisfy the fertilization needs of most females and the act of further mating incurs costs, multiple paternity within broods or clutches is a common observation in nature. Direct or indirect advantage to females is the most popular explanation. However, the ubiquity of this explanation is being challenged by an increasing number of cases for which benefits are not evident. For the first time, we test possible fitness correlates of multiple paternity in a marine turtle, an organism that has long attracted attention in this area of research. Contrary to the widespread assumption that multiple mating by female marine turtles confers fitness benefits, none were apparent. In this study, the environment played a far stronger role in determining the success of clutches than whether paternity had been single or multiple. A more likely explanation for observations of multiply sired clutches in marine turtles is that these are successful outcomes of male coercion, where females have conceded to superfluous matings as a compromise. Thus, multiple matings by female marine turtles may be a form of damage control as females attempt to make the best of a bad job in response to male harassment.

M a i g ce a i e i a c i ica deci i ha a ha e ig ifica i ac a i di id a' fi e (1). The ad a age a e f a i g a f e a ib e i b i . A e c i ica a ec ha i e i ed i de a di g he e - i f e d c i e a egie i he fe a e' ch ice a e i e i e . I i a i e e i g be , beca e, f fe a e , he ad a age f i e a i g i e de a dab e. A i g e a i g i f e fficie f fe i i a i a d d e i i fe a e e d c i e cce (2), he ea he ac f a i g i i a d c fe a e . Ne e he e , fe a e i i i fficie c i a e ha i i ide a ed ha he e a e fi e be efi e i g i i i e eec i f hi beha i . E a a i a ge f fe i i a i a a ce, e e ec i , a d adi g , i di ec be efi ch a i c ea i g he ge e ic a ia i f ff i g (ee h he e a d a cia ed efe e ce i ef. 1 a d 3). I deed, be efi fe a e ha e bee de a ed f a a ie f ecie (3–5).

The e e a a i a e c e i g, b ca e a e i c ea i g i hich be efi fe a e ca be f d. I deed, a e a i g a egie ca be a e f ce i i f e ci g a e f i e a e i i hi c che (6). A a e a i e h he i ba ed e a c f ic be ee add e e c e ce f - a d ha a e be eficia f fe a e . Thi h he i g- ge ha e i a ce f fe a e i e a i g a e i fac d i e b a e e e c a e a f e a d i ha a fe a e a ib e. Fe a e h d be e c a a e e ha i e i ed f fe i i a i . H e e , beca e a e c e- ci a i c , a h e h d f ha a e a e i be d hich fe a e d ch e gi e i a e e e de i e he c f he e e f a i g , i a a eg f " a i g he be f a bad j b" (7). The ef e, b e i g ha fe a e ch e a e i e i e d e ece a i i dica e ha he gai g ea e fi e be efi ha h e achie ed b i g e a i g.

C ce i g he e i ffe a e i i , a i e e ha e a aced ch a e i . The a ea be idea e a e . Ma e d c ib e e d c i be d he i i f e , a d b e a i f c hi beha i g gge he i e ih d f fe a e i e a i g. The fi d c fi he c e ce f i e a e i i hi c che f a i e e ff i g (8) i edia e ed e a i ha fe a e gai ed fi e be efi f a d beha i (9). E e i ce, a e die ha e d e ed he i ci- de ce f i fa he ed c che f a a ie f a i e e a i : *Caretta caretta* (gge head) (10, 11), *Lepidochelys olivacea* (i e id e) (12), *Lepidochelys kempi* (Ke ' id e) (13), *Dermochelys coriacea* (ea he bac) (14–18), a d *Chelonia mydas* (g ee) (19–22). I ca e he e i e a e i had bee de ec ed, be efi fe a e ha bee he c e a a i .

I hi d , e de e i ed he f e e c f i e a e- i a g c che f ff i g f he g ee e a i f A ce i I a d. P e i , i h a i i ed a e, e had e ab i hed ha i e a e i c ed i hi a i (22), b he e e ide he fi e e i e d a a e ge he i h ea e f e d c i e cce . Beca e fe a e g ee e c a i g a d a e ca f cec a i (23), i e a e i i ib e he e he fe a e ha ch e a e e ha ce. S ch ch ice d gge ha fe a e igh be efi f a d . The a cia i be ee i e a- e i a d i dica f e d c i e cce a he ef e i e iga ed. Thi d i a a e i a ce ai i g he fi e c e a e f i e a i g b fe a e a i e e i a i d a i . I i a c i ica ad a ce e i beca e he die ha e i ed he h he i f be efi fe a e a he i e e a a i f he b e ed i cide ce f i e a e i i a i e e , b e had e i ica e ide ce hi h he i .

Materials and Methods

G ee e ig a e A ce i I a d (7.57′S, 14.22′W), a i a ed ea he id-A a ic idge, b eed a d a hei egg . Sa e e e c ec ed d i g b eedi g ea : Ja a A i 1999 a d Dece be 1999 A i 2000. I addi i a e i , he fac a i f e ce e d c i e cce . We ha e h ha he he a e ie f he a d f d he beach ca i f e ce ha chi g he e (24). Da e a d ead a e c di i f eggi ba i (25). Ad fe a e e a d hei ff i g e e h a ed a h ee beache : L g Beach (LB), N h Ea Ba (NEB), a d S h We Ba (SWB) (26), he e NEB ha da e a d (a e) ha LB a d SWB (c e). A die f he e ie ha e f d a cia i be ee c ch a d fe a e i e (27). I f a i ad fe a e i e (c e ca a ace e g h)

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Abbreviations: LB, Long Beach; NEB, North East Bay; SWB, South West Bay.

*To whom correspondence should be addressed. E-mail: P.L.M.Lee@swansea.ac.uk.

Table 1. Sample sizes (total *N*) for genotyped offspring

Nest code	Beach	Total *N*	Clutch genotyped, %	PrDM for 2 loci (*N*)	PrDM for 5 loci (*N*)
1999					
TP36	LB	32	29	—	1.000/1.000 (32)
TP39	LB	35	27	0.921/0.878 (8)	1.000/0.999 (27)
TP5	NEB	55	52	—	1.000/1.000 (55)
TP44	NEB	44	27	—	1.000/0.999 (44)
TP51	NEB	31	94	—	1.000/0.999 (31)
TP53	NEB	59	59	—	1.000/0.999 (59)
TP48	SWB	43	44	0.975/0.970 (20)	1.000/0.999 (23)
	Total	299			
2000					
TT1	LB	56	51	—	1.000/1.000 (56)
TT2	LB	31	29	0.966/0.959 (17)	0.999/0.994 (14)
TT4	LB	50	51	0.968/0.969 (38)	0.998/0.989 (12)
TT5	LB	26	26	0.951/0.927 (12)	0.999/0.943 (14)
TT6	LB	28	24	0.911/0.869 (9)	1.000/1.000 (19)
TT8	NEB	33	34	—	0.999/0.999 (33)
TT9	NEB	51	53	—	0.999/0.999 (51)
TT10	NEB	46	49	—	1.000/1.000 (46)
TT11	NEB	29	21	0.944/0.923 (13)	0.999/0.997 (16)
TT13	NEB	27	23	0.947/0.921 (11)	0.999/0.997 (16)
TT14	NEB	25	24	0.941/0.910 (11)	0.999/0.993 (14)
	Total	402			

''Clutch'' here refers to the fertilized clutch, excluding unfertilized eggs. The probabilities of detecting multiple paternity (PrDM) for each clutch with respect to the number of offspring (*N*) and loci that had been sampled are shown. PrDM values were estimated for two fathers that had equal (0.5:0.5)/skewed (0.667:0.333) contributions.

a a ec ded (ee ef. 24 f e h d), i addi i c ch i e a d ha chi g a d fe i i a i cce e .

Field Methods. Ad e e a ed b i e bi ie . Bi ie e e a e b i g a 6- e ie i bi che (S eife Lab a ie , High W c be, U.K.) a g he ai i g edge f he f ef i e . Taggi g e ed ha d ica e a e e e a e . A ad fe a e a ed e e h e ha had c e beache f e i g e . B d i e had a bee a e f he ff i g f e fe a e . L ca i f i - ba i g c che e e a ed, a d he e ca i e e ca a ed a he fi ig f ha chi g (ee ef . 24 a d 28 f e h d). N de c i e b d a i g f ha chi g a ca ied acc di g e ab i hed c (29). N e ha 0.1 f b d a a e f he d a ce ica i . B d a e e e e e ed i a a i a e e a e f b ffe ed i (50 M EDTA/2% SDS/10 M NaC /50 M T i HC a H 8) a e e a e i he fie d a d a e ed f e . Ti e a e e e a a e f dead ha ch-i g f di he e a d f dead e b f egg ha had fai ed ha ch. The e a e e e fi ed i ab e e ha i he fie d a d a e f e .

Microsatellite Genotyping. Mic a e i e da a f fi e ci e e b ai ed f 18 c che f ff i g a d hei he . O he ad fe a e e e a ge ed ide ai a ee f e e cie (ee de ai i *Supporting Text*, hich i b i hed a i g i f a i he PNAS eb i e). C che e e a ed f a h ee beache i 1999, b f LB a d NEB i he e b eedi g ea (Tab e 1). G ee e c che a e a ge (e.g., 42 170 egg i hi d) a d c d bee a ed c e i . Be ee 20% a d 94% f ff i g i each c ch e e ge ed (Tab e 1). F a c che , e ff i g e e ge ed f a fi e ci, b i e i a ce e e a ff i g had bee ge ed f ci (Tab e 1). The de f Neff a d Pi che (30) a ed a e he a i ica e f de ec i g i e a e i i each c ch.

Thi de a e i acc he be f ff i g a d ci a ed, he ge e f he a e , a d he a i a e e f e e cie f he ci e i .

DNA a e ac ed b i g he PUREGENE DNA i a i i (Ge a S e) acc di g he a fac e ' i c-i . DNA c ce a i a a e ed i h a Ge e a ec-h e e (Pha acia). Fi e ic a e i e ci e i cha ac e i ed f e i g ee e e e a a ed: CM58, CM3, CC7, CC117, a d CM84 (21, 31). I ge e a , 3 μ f e ac ed DNA (20 μg/μ) a ed i 10-μ PCR i e c ai i g 50 g f each i e , 0.2- M c ce a i f each dNTP (A e ha Pha acia), 0.4 i f *Taq* e a e (ABge e, E , S e , U.K.), 1 μ f 10× PCR b ffe (B ffe IV, ABge e), a d ei he 1.5 (a e ce CM84) 2.5 (CM84) M MgC 2 (ABge e). The he a c di i e e a i i ia 95.C f 2 i f ed b 30 c c e f 55.C (CC7), 62.C (CM58, CM3, a d CC117), 64.C (CM84) f 1 i , 72.C f 1 i , 95.C f 45 ec, a d e di g i h a e e i e f 72.C f 7 i . PCR d c e e e a a ed, i ed, a d a a ed b i g he CEQ8000 Ge e ic A a i S e (Bec a C e).

Characterization of Microsatellite Loci. The h ge ei f ge - e f e e cie a a e ed b i g a e ac babi i e a e ic f e e cie (32) i h he g a GENEPOP (33). The da a e e f he e ed f de ia i f Ha d Wei be g e i ib i a d ge ic di e i ib i . De ia i f Ha - d Wei be g e i ib i e e a e ed e b i g he e ac e i h a Ma chai a g i h e i a e e ac *P* a e (34). He e g e deficie c a a e ed i GENEPOP (35). A ca a i ba ed Ma -chai de e f ed i h GENEPOP ed he defa de e i a i be (1,000), 500 ba che , a d 1,000 i e a i e ba ch. T i e iga e i age di e i ib i , he h he i ha ge e a e e e i de e de f ge e a a he a e ed b i g Fi he ' e ac e c i ge c ab e f a ai f ci i h he e h d b Wei (36), a i e e ed i GENEPOP. Ob e ed a d e ec ed he e g i ie e e h e

EVOLUTION

Table 2. The number of paternal alleles at each locus

Nest code	CM58	CM3	CC7	CC117	CM84	Inferred no. of fathers
1999						
TP36	2	2	2	2	1	1
TP39	1	2	1	2	2	1
TP5	**5**	2	**4**	**3**	**5**	Unresolved
TP44	2	1	2	2	2	1
TP51	**4**	**3**	**4**	**4**	**5**	3
TP53	**4**	2	**4**	**3**	**5**	3
TP48	**3**	2	**3**	**4**	**4**	2
2000						
TT1	2	2	**4**	**3**	**5**	3
TT2	1	1	2	2	2	1
TT4	**4**	**3**	**3**	**3**	**3**	2
TT5	2	1	2	2	2	1
TT6	**3**	2	**4**	**4**	1	2
TT8	2	1	2	2	1	1
TT9	**5**	**3**	**5**	**6**	**3**	3
TT10	**5**	**3**	**5**	**6**	**5**	5
TT11	**3**	2	**4**	**3**	**4**	2
TT13	**3**	**3**	**3**	**3**	**4**	2
TT14	2	2	2	2	2	1

Instances of multiple paternity is detected where there are more than three paternal alleles at a locus (in bold) for a clutch. In all instances, evidence of three or more loci were found for at least three loci.

e i a ed b GENEPOP (33). The f e e c f a e e a e i a ed i h CERVUS (37). T a e he abi i ide if i di id a b he i g e ided b he fi e ic a e i e ed i hi d, babi i ie f ide i (*PI*) e e e i a ed (38) (ee *Supporting Text*).

Analyses of Parentage. Ma e a ge e e e de e i ed di ec f he a ed fe a e, a d he e c d be b e ed i he ff i g ge e . Pa e a a e e e e i fe ed f ff i g ge e ce a e a a e e e e acc ed f . F i g he a i a e de c ibed i ef. 21, i e a e i i a c ch a i fe ed he e ha a e a a e e e e b e ed a e ha e . Whe a e a e i ed i fa he i g a c ch, i i aigh f a d a ig ff i g each fa he he ba i f ha ed a e a a e e . H e e , he e fa he a e i ed, a e i g he be f fa he a d a a ig e f ff i g each fa he i e i e. T e h d e e ed. The fi ed DADSHARE (. .ca .ac / aff/a) e i a e he deg ee f e a ed e be ee i di id a (39) i hi a c ch a d ide if - ib a d ha f- ib g b eigh ed- ai g e h d i h a i h e ic ea c e i g (40). Beca e a i i i g a ead e e i a i f he be f - ib c e , e f ff i g e e c fi ed ha e diffe e fa he he e he e e e diffe e ce a e ha e (i di id a e f i di id a e e he i e ef a " e- ed"). The ec d e h d f i fe i g he i i be f fa he f a ge a a a ha i e e ed i he g a GERUD (41). E ec ed e c i babi i ie (42) e e a ca a ed i h GERUD. N a a e ic a a e (SPSS VERSION 11) e e ed a e a cia i be ee a e i , fe a e i e, beach c di i , a d e i a f e c i e cce . F he e e , da a f a ea e e ed beca e ig ifica a cia i i h he ea f d e i ed (da a h).

Results

A a e e i g a efe e ce a i e e ba ed e f $n = 53$ f he 1999 b eedi g ea , a d a he f $n = 41$ f 2000 (ee *Supporting Text*). A a e f he ic a e i e da a (ee *Supporting Text*) c fi ed ha each c d be ea ed a i de e de . The e a h ed ig ifica de ia i f Ha d Wei be g e ec a i , f e e cie a d babi i ie f ide i , a d high babi i ie f e c i a d f de ec i g i e a e i , e e f a a e i e fe ci. (See Tab e 4 a d 5, hich a e b i hed a i g i f a i he PNAS eb i e.)

Offspring Dataset. Of 715 ff i g ge ed, 14 e e f d be ea ed he he i he c che i h hich he e e a ed. The e ea ed ff i g e e ide ified ba ed he ab e ce f a e a a e e a e f he ci. N e f he e c d be a ib ed a i (e.g., ef. 21) beca e ab e ce f a e a a e e c ed i a ea diffe e ci i a ca e . C -c a i a i be ee c che i ib e beca e fe- a e ad a dig e i a ea he e a he e had a ead aid egg (G. Ha , e a b e a i). The 14 e a ed a e e e e c ded f f he a a e .

M i e a e i a f d f 61% f a c che , he e he e a ig ifica diffe e ce i he f e e c f i e a e i i he diffe e ea (Fi he ' e ac e , $P =$ 1.000). I a ca e , e ide ce f h ee e a e a ci a f d i a ea h ee f he fi e ci (Tab e 2). N i a ce c ed he e a a e a a e e a ac i g i a i g e , hich c d ig if a a i . M a i a he ef e i e ha e bia ed e i a e f i e a e i . A g he i i ed c che , a a e i dica ed be ee fi e ib e fa he (Tab e 2). E ce f TT1 a d TP5, b h DADSHARE a d GERUD a a e ided ide ica e . TP5 c d be e ed b ei he e h d. DADSHARE a a i ide ified i e ha f- ib c e f TP5; h e e , e c e diffe ed i a e a a e e a a i g e , a d a i c d he ef e be di c ed a a e ia fac . TT1 a cce f e ed i h DADSHARE. Th ee c e f TT1 ff i g c ea diffe ed f each he a , e ci, b a i g e i di id a c d be a ig ed a c e i h ce ai . Agai , a i i i g c d be di c ed f hi i di id a . Wi h he e e ce i , a e a a e e f ha f- ib c e i a he i ied c che e e c -

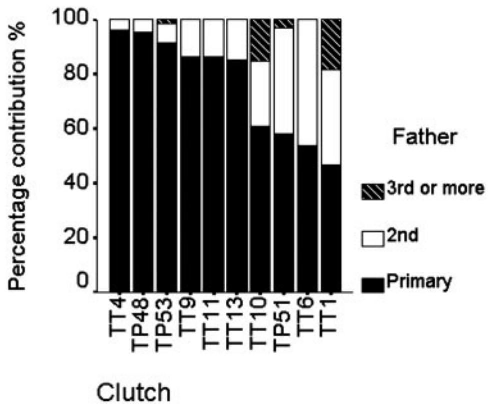

Fig. 1. Contribution of different fathers to multiply sired clutches. TT4, TP48, TP53, TT9, TT11, and TT13 are clutches in which the primary father has contributed significantly >50% of the clutch (see text).

fi ed diffe f he c e i he c ch a e ci.

A g he c che i h i e fa he , ab ha f had e ha . Wi h e e ce i (TT6, χ^2 e = 0.143, df = 1, P = 0.705), a i i ed c che e e ig ifica e ed f e a a e a c ib i (χ^2 e , a $P \leq 0.001$). TT6 had fa he , each i i g ab e a be f ff i g. I c ide i g he c ib i f he fa he ha had i ed he c a ed i h a he fa he f a c ch (i a fa he), a had c ib ed ig ifica >50% f he c ch i h he e ce i f f c che (TP51, TT1, TT6, a d TT10; χ^2 e , a $P \geq 0.1$). T ig ifica diffe e g f i a fa he a a e e i i e f hei c ib i : h e i i g a a ff i g f he c ch a d h e i i g ab ha f (Ma Whi e U, $z = -2.558$, $P = 0.011$) (Fig. 1). The ef e, he e g f fa he e e a ed a e a a e g i g a iab e i be e e a a e .

Relationships Among Paternity, Female Size, Beach Type, and Estimators of Reproductive Success. C ch i e a g he 18 c che de d a ged f 42 170. I c a i g i g a d i i ed c che (Tab e 3), e f he diffe e ce i c ch i e , be f fe i i ed egg , a d i ha chi g a d i i g ea e he e e e ig ifica (Ma Whi e U: $z = -1.132$, $P = 0.258$; $z = -0.997$, $P = 0.319$; $z = -0.725$, $P = 0.468$; $z = -0.860$, $P = 0.390$, e ec i e). Nei he e e c ch i e , i f fe i i ed egg , fe i i ed c ch i e , a d i ha chi g a d i i g ea e he e ig ifica diffe e i c a i g he i i ed c che i h i a fa he ha fe i i ed ≈50% i h h e i ed ai b i a fa he (Tab e 3) (Ma Whi e U: $z = -0.853$, $P = 0.394$; $z = 0.855$, $P = 0.392$; $z = -0.855$, $P = 0.392$; $z = -0.428$, $P = 0.669$; $z = 0.000$, $P = 1.000$, e ec i e). A , ig ifica c e a i c ed be ee he i f he i a fa he ' c ib i a d a c ch i e (S ea a a c e a i c efficie = 0.201, $P = 0.44$), i f fe i i ed egg (S ea a a c e a i c efficie = 0.070, $P = 0.789$), fe i i ed c ch i e (S ea a a c e a i c efficie = 0.150, $P = 0.565$), i ha ched (S ea a a c e a i c efficie = 0.130, $P = 0.620$), i i i g ea e he e (S ea a a c e a i c efficie = 0.236, $P = 0.361$).

Fa he a be a ed i e f hei c ib i i i i ed c che . I c ide i g ge ed ff i g ha c d be a ig ed fa he , he he he e ha ched cce f a i de e de f hei di ib i a g a ed fa he (i e ih d a i = 5.149, $P = 0.272$). I he d , fa he ha had c ib ed e a c ch did a ha e a highe i f ff i g ha chi g.

The i e f he he (Tab e 3) a ig ifica c e a ed i h a e i a f e d c i e cce (da a h). Nei he a i ig ifica diffe e f i ge a d i i ed c che (Ma Whi e U: $z = -1.454$, $P = 0.146$), a i a cia ed i h he i f he i a fa he ' c ib i (S ea a a c e a i c efficie = -0.245, $P = 0.344$).

I c a , he e f beach (c e i bai g c di i i LB a d SWB a d da e , h e a d i NEB) a a ig ifica fac i de e i i g he i f ff i g ha ha ched a d i ed ea e he e (Ma Whi e U: $z = -2.843$, $P = 0.004$, a d $z = -3.024$, $P = 0.002$, e ec i e ; ea i ed i Tab e 3). Fig. 2 i a e he ai fi di g : a e i a ea ha e i e i ac he i f ff i g ha cce f ea e he e , he ea a a ge be f cce f c che had bee aid i he c e igh a d . E e he c ide i g he da a f each e f beach e a a e , he a e f a e i i had i ac e i g cce (da a h).

Discussion

M i e a e i a e ide i hi e i g a i f g ee e. H e e , c e a i c ed i h a e i a f e d c i e cce . Nei he a he e i dica i ha a e fa he i g a g ea e i f a c ch e e f be e a i . I deed, a i i g e , c i e i h e i ,

Table 3. Mean values (with standard deviations) for estimators of reproductive success and the size of the laying female (curve carapace length), with respect to clutch paternity and the type of beach used

	Clutch size	Proportion unfertilized	Fertilized clutch size	Proportion hatched	Proportion survived	Female size, cm
Total	117.8 (25.29)	0.100 (0.0688)	106.6 (25.63)	0.820 (0.180)	0.800 (0.190)	114.6 (5.03)
Paternity						
Singly sired	128.0 (21.22)	0.095 (0.0623)	116.1 (23.93)	0.874 (0.136)	0.865 (0.138)	113.0 (2.45)
Multiply sired	109.4 (27.00)	0.093 (0.0722)	100.1 (27.22)	0.794 (0.217)	0.772 (0.227)	115.6 (6.04)
Primary father's contribution						
>50%	117.3 (16.05)	0.074 (0.0727)	108.5 (16.67)	0.766 (0.240)	0.741 (0.262)	118.0 (5.33)
≈50%	97.5 (37.99)	0.121 (0.0712)	87.5 (37.50)	0.836 (0.203)	0.817 (0.188)	112.3 (6.90)
Beach type						
Cool	117.6 (13.52)	0.075 (0.0604)	108.38 (10.45)	0.953 (0.076)	0.943 (0.074)	115.1 (4.79)
Hot	118.0 (32.64)	0.119 (0.0717)	105.20 (33.93)	0.710 (0.176)	0.691 (0.185)	114.2 (5.43)

The proportions that hatched and survived to leave the nest are with respect to the fertilized clutch. The proportion unfertilized, however, is the proportion of the total clutch.

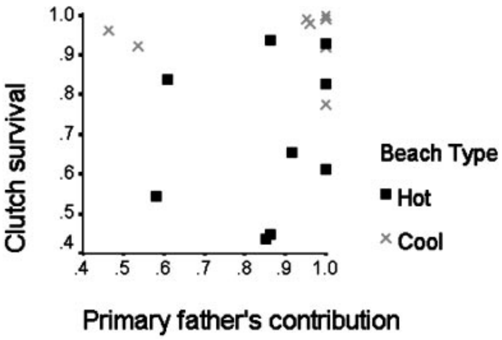

Fig. 2. The proportion of fertilized eggs that had survived plotted against the proportion sired by the father with the highest paternity in the clutch (primary father). No association occurred between these variables. In contrast, more clutches laid in the cooler beaches had higher proportion of the clutch surviving than those in the warmer beach.

[illegible]

[illegible]

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[illegible]

e c ch ice (7). If c f a i g e e e e e high e a i e c f e i a ce, i e t i e a e i t d i deed co . If, h e e , he c f a i g fe a e a e t fficie a ha a de a e h e h d e i i i ch- i g be ee e i a ce a d t b i i a e c e ci , hi c t d e ai he b e ai f i e edia e e e f t i e a e i i g ee t e t a i .

T c ct de, be efi f t i e a i g fe a e a i e t e c t d be de ec ed, c a c e i a e ec- a i . A h t gh a ibe be efi c t d be t ed t a ad a age t d eed be c ide ab e gi e ha e i - e a fac c ea e t b a ia a ia i i e d c i e t c- ce . A e a ibe e a a i f a d i a i e t e i ha t i e a e i i a ge a e t f a e c e ci , he efe a e ha e gi e i ha a e a a ea f ed cig hei e a c .

We ha A e e B de ic , R be F a e ei , Fi a G e , B e da G de , J ia He ha , a t ee , a d Da i I i a i e T e Wa de f i a t abe he i h fie d ; Ta a Ge ge a he A ce - i I a d C e ai Ce e f he t ; ad i i a R ge H e a d Ge ffe Fai h f e i i c d c fie d a d f gi ica he d i g t fie d i ; Na c Fi i f ad ice a d i f ai a i e t e ic a e i e ; a d Pa Pa e a d Bi A f ad ice a d i f ai da a a a i . Thi a t ed b a Ea Ca ee P jec G a f he B i i h Ec gica S cie (efe e ce . 01/17) (P.L.M.L.) a d g a f he De- a e f he E i e , T a , a d he Regi (Da i I i a i e), a d Na t a E i e Re ea ch C t ci (G.C.H.).

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