

# eDNA

Richard Arnold

2024-07-16

## Detection of eDNA

- A volume  $V_S$  of water is collected, and all of the eDNA it contains is collected by filtration. Assume a count  $N_j$  of eDNA fragments of type  $j$  is collected ( $j = 1, \dots, J$ ). If the number density of fragments in the water is  $\nu_j$  then

$$N_j | \nu_j, V_S \sim \text{Poisson}(\nu_j V_S)$$

- The collected eDNA is mixed with a volume  $V_M$  of a proprietary mix of primers, probes and water;
- A test volume  $V_T$  ( $1\mu\ell$ ) is taken from the mixture: The count of fragments in the test volume is

$$n_j | N_j, V_M, V_T \sim \text{Poisson}(N_j V_T / V_M)$$

- The test volume is atomised into  $m$  droplets. The count of fragments in droplet  $i$  is

$$y_{ji} | n_j, m \sim \text{Poisson}(n_j / m)$$

- The probability that droplet  $i$  has zero fragments is

$$\Pr(y_{ji} = 0 | n_j, m) = \exp\left(-\frac{n_j}{m}\right)$$

and thus the probability that it contains any fragments is

$$\Pr(y_{ji} > 0 | n_j, m) = 1 - \exp\left(-\frac{n_j}{m}\right)$$

- The eDNA in the droplets is amplified by PCR, and  $m_{j+}$  of the droplets are observed to be positive for fragment type  $j$ . Thus the observed proportion of positive droplets is

$$\hat{p}_+ = \frac{m_{j+}}{m}$$

and

$$m_{j+} | n_j, m \sim \text{Binomial}\left(m, 1 - e^{-n_j/m}\right)$$

or if  $n_j/m$  is very small then

$$m_{j+} | n_j, m \sim \text{Poisson}\left(m \left(1 - e^{-n_j/m}\right)\right)$$

Note that we assume no false positives and no false negatives when individual droplets are amplified and tested for the presence of the eDNA.

This process is aimed at determining  $\nu_j$ , the original number density in the water from which the sample was collected. A simple estimate of  $\mu_j$  is

$$\hat{\nu}_j = -\frac{V_M m}{V_S V_T} \log\left(1 - \frac{m_{j+}}{m}\right)$$

However in this application we are most interested in the probability that the process leads to negative result when  $\nu_j$  is non-zero. i.e. we want to know

$$\Pr(m_{j+} = 0 | m, V_S, V_T, V_M, \nu_j) \quad (1)$$

$$= \sum_{N_j=0}^{\infty} \sum_{n_j=0}^{\infty} \Pr(m_{j+} = 0 | n_j, m) \Pr(n_j | N_j, V_M, V_T) \Pr(N_j | \nu_j, V_S) \quad (2)$$

$$= \sum_{N_j=0}^{\infty} \sum_{n_j=0}^{\infty} \exp\left(-m \left[1 - e^{-n_j/m}\right]\right) \exp\left(-\frac{N_j V_T}{V_M}\right) \frac{\left(\frac{N_j V_T}{V_M}\right)^{n_j}}{n_j!} \exp(-\nu_j V_S) \frac{(\nu_j V_S)^{N_j}}{N_j!} \quad (3)$$

Note that the sum over  $n_j$  should only be from 0 to  $N_j$ , but we sum to infinity because the additional terms are all negligible.

Writing the ratio  $V_T/V_M$ , i.e. the proportion of the mixture that is atomised and tested, as  $d$ , and suppressing the index  $j$

$$\Pr(m_+ = 0 | m, V_S, d, \nu) \quad (4)$$

$$= \sum_{N=0}^{\infty} \sum_{n=0}^{\infty} \Pr(m_+ = 0 | n, m) \Pr(n | N, d) \Pr(N | \nu, V_S) \quad (5)$$

$$= \sum_{N=0}^{\infty} \sum_{n=0}^{\infty} \exp\left(-m \left[1 - e^{-n/m}\right]\right) e^{-Nd} \frac{(Nd)^n}{n!} e^{-\nu V_S} \frac{(\nu V_S)^N}{N!} \quad (6)$$

At very low concentrations

$$n | \nu, V_S, d \sim \text{Poisson}(\nu V_S d)$$

so that

$$\Pr(m_+ = 0 | m, V_S, d, \nu) \quad (7)$$

$$= \sum_{n=0}^{\infty} \Pr(m_+ = 0 | n, m) \Pr(n | \nu, V_S, d) \quad (8)$$

$$= \sum_{n=0}^{\infty} \exp\left(-m \left[1 - e^{-n/m}\right]\right) e^{-\nu V_S d} \frac{(\nu V_S d)^n}{n!} \quad (9)$$

$$= \sum_{n=0}^{\infty} \exp\left(-m \left[1 - e^{-n/m}\right]\right) e^{-\lambda} \frac{\lambda^n}{n!} \quad (10)$$

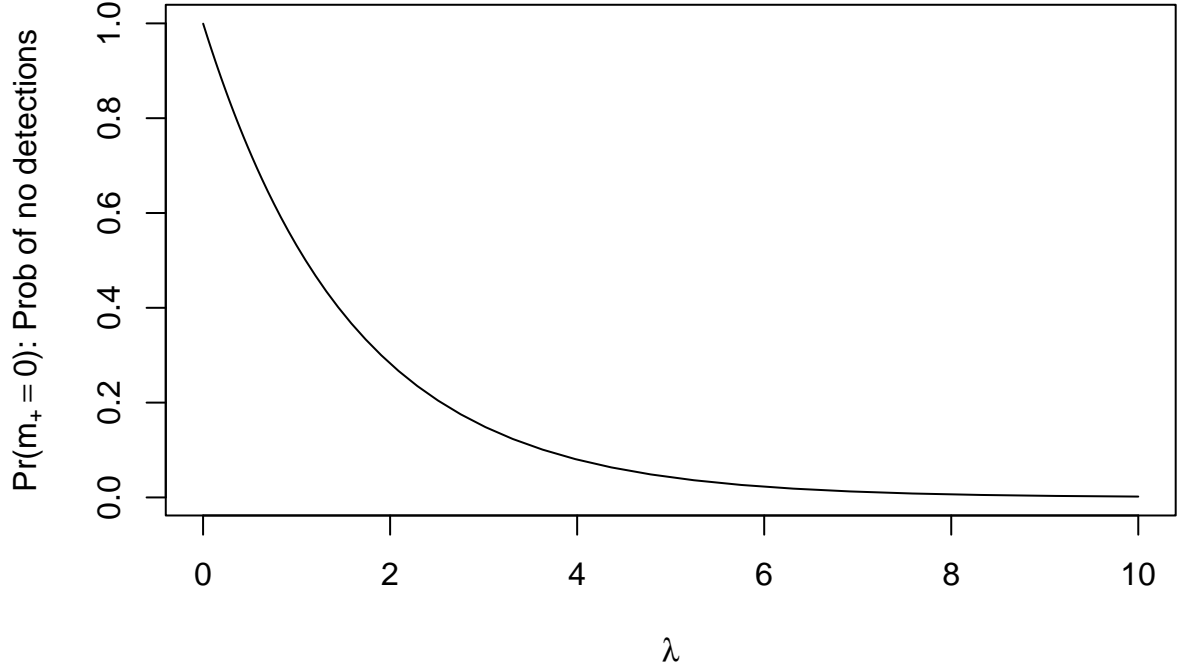
$$(11)$$

where  $\lambda = \nu V_S d$ .

Typically we have  $m = 2 \times 10^4$  droplets. We might expect  $\nu V_S \simeq 10$  fragments to be captured, and a subsampling of  $d = 1/20$ , and in that case  $\lambda \simeq 0.5$

```
probm0 <- function(lambda, m=20000, nbig=20000) {
  nvec <- 0:nbig
  fval <- sapply(lambda, function(lambdav) sum(exp(-m*(1-exp(-nvec/m))))*dpois(nvec,lambdav)))
  return(fval)
}
m <- 20000; nbig <- m
np <- 101
lambdavec <- 10^(seq(from=-3,to=+1,length=np))
plot(lambdavec, (probm0(lambdavec, m=m, nbig=nbig)), type="l",
     xlab=expression(lambda), ylab=expression("Pr("m["+"]="0*"): Prob of no detections"),
     main=bquote(lambda==nu*V[S]*d*"; "m*"]="*. (m)*" droplets"))
```

$\lambda = vV_{sd}$ ;  $m=20000$  droplets



## Particle dispersal

If there is a mass released at time  $t_0$  at location  $\mathbf{x}_0$  then it is transported by advection (water flow) and dispersion (turbulence).

Let  $p(\mathbf{x}, t | \mathbf{x}_0, t_0, \mathbf{v}(), \mathbf{a}(), \Psi)$  be the proportion of the mass released that is found at location  $\mathbf{x}$  at time  $t$ , given water flow  $\mathbf{v}()$  and dispersion  $\mathbf{a}()$ .  $\Psi$  is a set of additional parameters controlling the flow/dispersion model.

A simple model is a simple Gaussian spread in 2D:

$$\begin{aligned}
 p(\mathbf{x}, t | \mathbf{x}_0, t_0, \mathbf{v}, \mathbf{a}, \Psi) &= \frac{I(t - t_0 \geq 0)}{2\pi\sqrt{a_x a_y}(t - t_0 + t_\varepsilon)} \exp\left(-\frac{(x - x_0 - v_x(t - t_0))^2}{2a_x(t - t_0 + t_\varepsilon)} - \frac{(y - y_0 - v_y(t - t_0))^2}{2a_y(t - t_0 + t_\varepsilon)}\right) \\
 &= g(\mathbf{x}, t - t_0 | \mathbf{x}_0, \mathbf{v}, \mathbf{a}, \Psi)
 \end{aligned} \tag{13}$$

where a small positive temporal offset  $\Psi = \{t_\varepsilon\}$  is added to avoid a singularity at  $t = t_0$ .

We have

$$\iint p(\mathbf{x}, t | \mathbf{x}_0, t_0, \mathbf{v}, \mathbf{a}, \Psi) d\mathbf{x} = 1$$

for all times  $t > t_0$ .

Note that  $g()$  has a symmetry in which we can interchange  $\mathbf{x}$  and  $\mathbf{x}_0$  and at the same time reverse the velocity field, so for any time interval  $u \geq 0$ :

$$g(\mathbf{x}, u | \mathbf{x}_0, \mathbf{v}, \mathbf{a}, \Psi) = g(\mathbf{x}_0, u | \mathbf{x}, -\mathbf{v}, \mathbf{a}, \Psi) \tag{14}$$

```
source("funcs.R")
```

```
nx <- 101
ny <- 101
xmin <- 0; xmax <- 100
```

```

ymin <- 0; ymax <- 100
xvec <- seq(from=xmin, to=xmax, length=nx)
yvec <- seq(from=ymin, to=ymax, length=ny)

x0 <- mean(c(xmin,xmax))
y0 <- mean(c(ymin,ymax))
t0 <- 0
vx <- 5; vy <- 1
ax <- 2^2; ay <- 4^2
teps <- 0.01

```

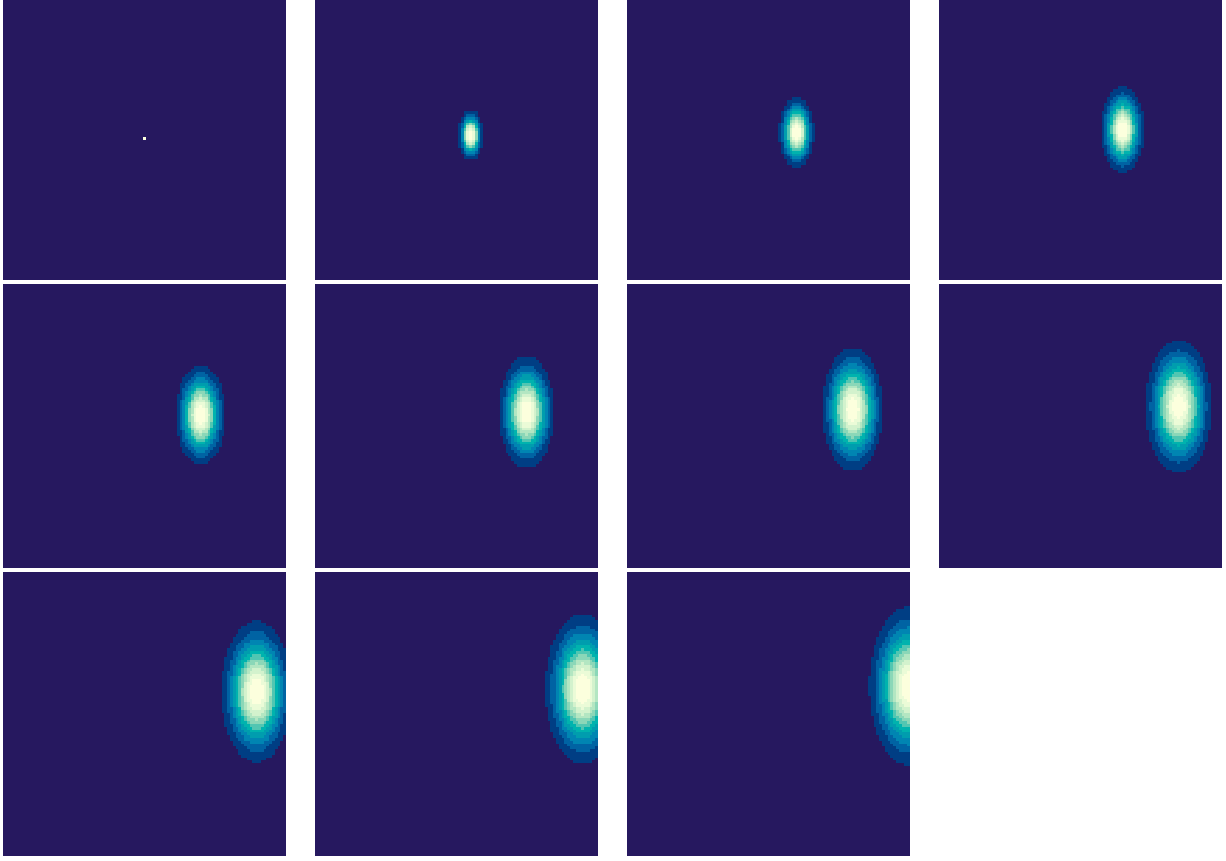
For example here is the spread over time of mass released at  $\mathbf{x}_0 = (50, 50)^T$  at time  $t = 0$  with constant flow field  $\mathbf{v} = (5, 1)^T$  and dispersion  $\mathbf{a} = (4, 16)^T$  and with  $t_\varepsilon = 0.01$ .

**Forward tracking:**  $p(\mathbf{x}, t | \mathbf{x}_0, t_0, \mathbf{v}(), \mathbf{a}(), \Psi): t_0, \dots, t_0 + 10$  (no decay)

```

par(mfrow=c(3,4))
par(mar=0.1*c(1,1,1,1))
colvec <- hcl.colors(12, "YlOrRd", rev = TRUE)
colvec <- hcl.colors(12, "YlGnBu")#, rev = TRUE)
for(t in 0:10) {
  amat <- outer(xvec,yvec, dispfunc, t=t,
               x0=x0,y0=y0,t0=0, vx=vx,vy=vy, ax=ax,ay=ay, teps=teps)
  #if(t==0) amax <- max(amat)
  amax <- max(amat)
  breaks <- seq(from=0, to=amax, length=length(colvec)+1)
  image(xvec, yvec, amat, asp=1, col=colvec, breaks=breaks, axes=FALSE)
  #image(xvec, yvec, amat,asp=1, main=bquote("Forwards:" ~ t==.(t)), xlab="x", ylab="y",
  #      col=colvec, breaks=breaks)
}

```



A simple backtracking model simply reverses the flow field. If we are interested in the likely origin of mass observed at location  $\mathbf{x}_1$  at time  $t_1$  we can backtrack by reversing  $\mathbf{v}()$ .

We might assume that the likelihood that the observed mass was released at location  $\mathbf{x}$  at time  $t < t_1$  is given by

$$\tilde{p}(\mathbf{x}, t | \mathbf{x}_1, t_1, \mathbf{v}(), \mathbf{a}(), \Psi) = g(\mathbf{x}, t_1 - t | \mathbf{x}_1, -\mathbf{v}(), \mathbf{a}(), \Psi) \quad (15)$$

$$= p(\mathbf{x}, -t | \mathbf{x}_1, -t_1, -\mathbf{v}(), \mathbf{a}(), \Psi) \quad (16)$$

In the simple Gaussian model above this is

$$\tilde{p}(\mathbf{x}, t | \mathbf{x}_1, t_1, \mathbf{v}(), \mathbf{a}(), \Psi) \quad (17)$$

$$= p(\mathbf{x}, t_1 | \mathbf{x}_1, t, -\mathbf{v}(), \mathbf{a}(), \Psi) \quad (18)$$

$$= p(\mathbf{x}, -t | \mathbf{x}_1, -t_1, -\mathbf{v}(), \mathbf{a}(), \Psi) \quad (19)$$

$$= g(\mathbf{x}, t_1 - t | \mathbf{x}_1, -\mathbf{v}(), \mathbf{a}(), \Psi) \quad (20)$$

$$= \frac{I(t_1 - t \geq 0)}{2\pi\sqrt{a_x a_y}(t_1 - t + t_\varepsilon)} \exp\left(-\frac{(x - x_1 + v_x(t_1 - t))^2}{2a_x(t_1 - t + t_\varepsilon)} - \frac{(y - y_1 + v_y(t_1 - t))^2}{2a_y(t_1 - t + t_\varepsilon)}\right) \quad (21)$$

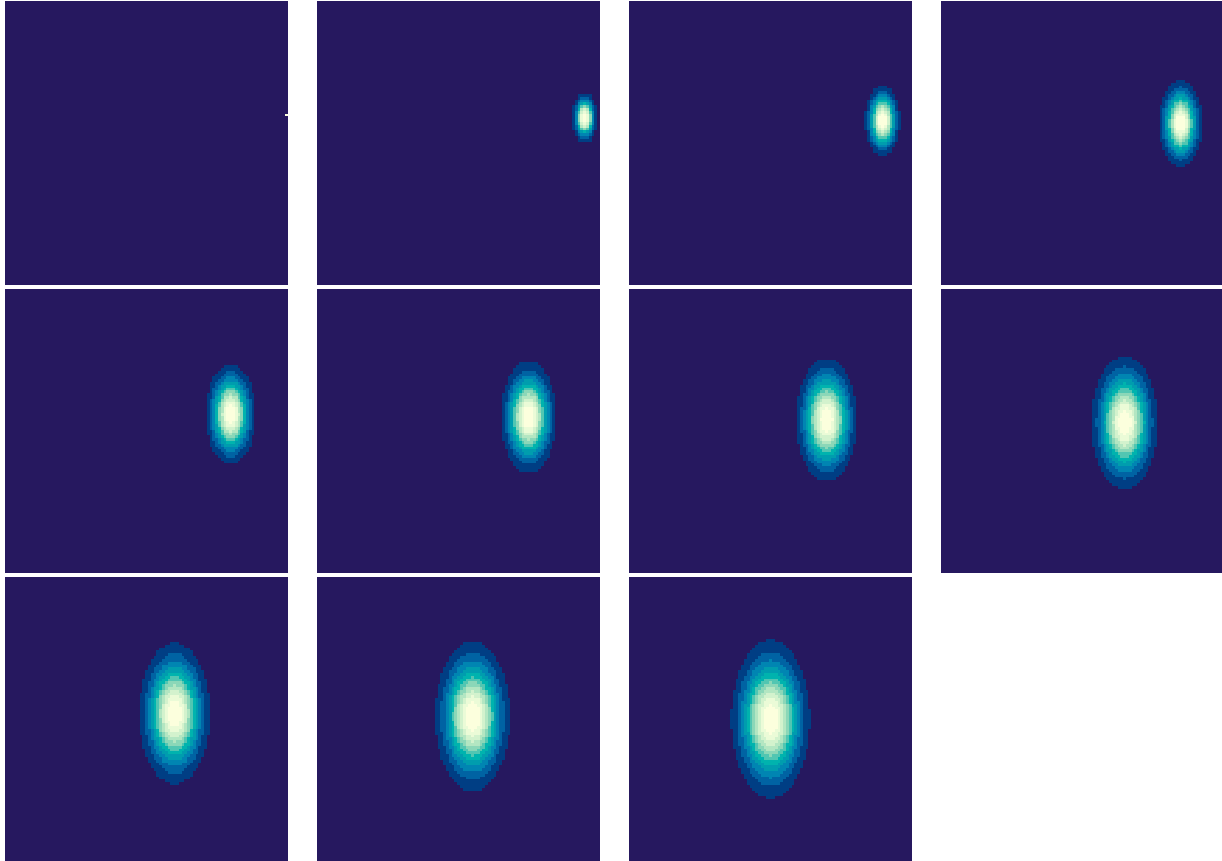
**Back tracking:**  $\tilde{p}(\mathbf{x}, t | \mathbf{x}_1, t_1, \mathbf{v}(), \mathbf{a}(), \Psi) = p(\mathbf{x}, -t | \mathbf{x}_1, -t_1, -\mathbf{v}(), \mathbf{a}(), \Psi)$ :  $t_1, \dots, t_1 - 10$  (no decay)

```
par(mfrow=c(3,4))
par(mar=0.1*c(1,1,1,1))
x1 <- 100; y1 <- 60
t1 <- 10
for(t in 10:0) {
  amat <- outer(xvec,yvec, dispfunc, t=-t,
```

```

        x0=x1,y0=y1,t0=-t1, vx=-vx,vy=-vy, ax=ax,ay=ay, teps=teps)
#if(t==10) amax <- max(amat)
amax <- max(amat)
breaks <- seq(from=0, to=amax, length=length(colvec)+1)
image(xvec, yvec, amat,asp=1, col=colvec, breaks=breaks, axes=FALSE)
#image(xvec, yvec, amat,asp=1, main=bquote("Backwards: " ~ t==.(t)), xlab="x", ylab="y",
#      col=colvec, breaks=breaks)
}

```



## Continuous release with decay

Assume that at location  $\mathbf{x}_0$  there is a continuous release of mass at a rate  $N_0$  kg/s. Further assume that the mass decays at a rate

$$d(t|T_h, T_m) = 2^{-t/T_h} I(0 \leq t \leq T_m)$$

where  $T_h$  is the decay half life and  $T_m$  is the maximum age at which all particles have disintegrated. If we set  $\lambda = (1/T_h) \log 2$  then

$$d(t|T_h, T_m) = e^{-\lambda t} I(0 \leq t \leq T_m)$$

The steady state mass in the system is then

$$M_0 = \int_{-\infty}^t N_0 d(t - t_0 | T_h, T_m) dt_0 \quad (22)$$

$$= N_0 \int_{-\infty}^t e^{-\lambda(t-t_0)} I(t_0 > t - T_m) dt_0 \quad (23)$$

$$= N_0 \int_{t-T_m}^t e^{-\lambda(t-t_0)} dt_0 \quad (24)$$

$$= N_0 \int_0^{T_m} e^{-\lambda u} du \quad (25)$$

$$= \frac{N_0}{\lambda} [1 - e^{-\lambda T_m}] \quad (26)$$

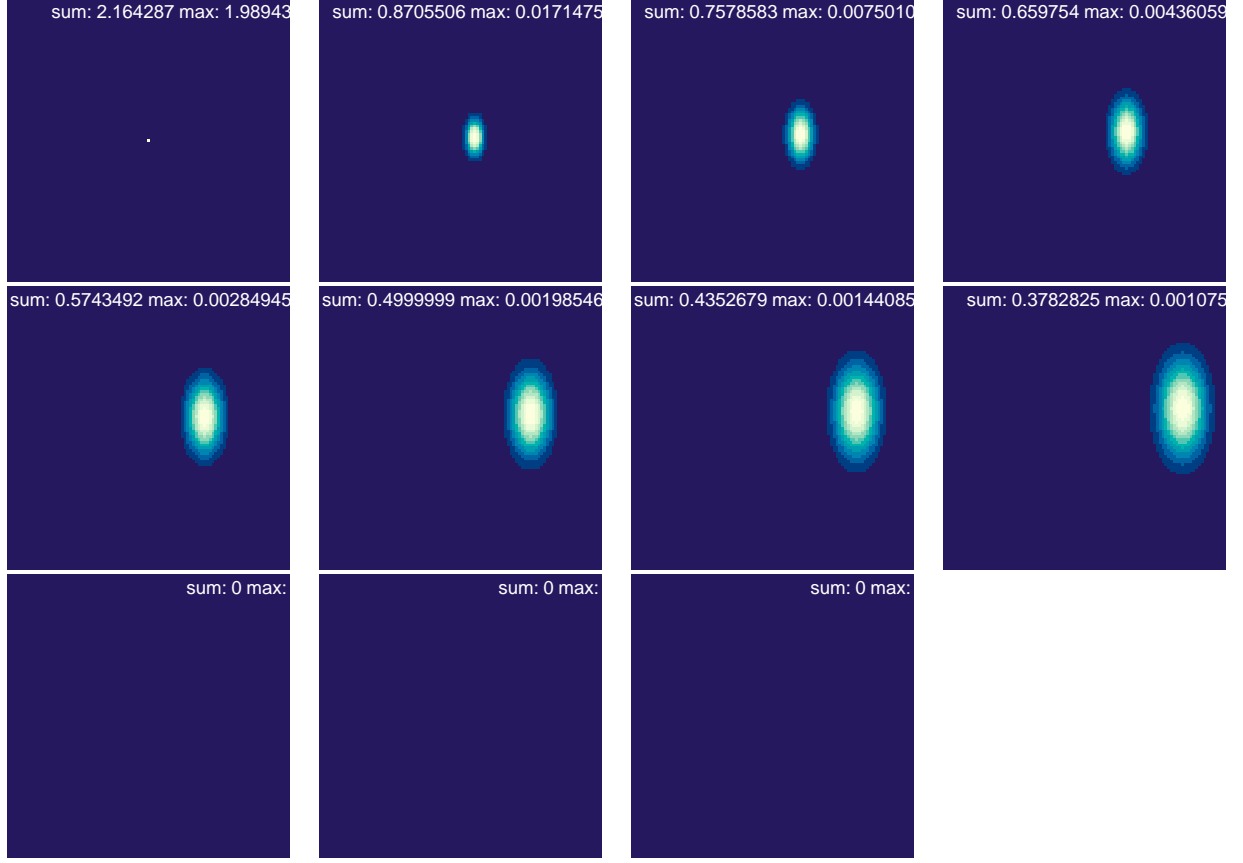
$$= \frac{N_0 T_h}{\log 2} [1 - e^{-\lambda T_m}] \quad (27)$$

The mass density transiting per unit time at location  $\mathbf{x}$  at time  $t$  emitted from a point source at  $\mathbf{x}_0$  at time  $t_0$  is

$$\frac{d\rho(\mathbf{x}, t | N_0, \mathbf{x}_0, t_0, \mathbf{v}(), \mathbf{a}(), \Psi)}{dt} = N_0 d(t - t_0 | T_h, T_m) p(\mathbf{x}, t | \mathbf{x}_0, t_0, \mathbf{v}(), \mathbf{a}(), \Psi)$$

**Density rate**  $d\rho(\mathbf{x}, t | N_0, \mathbf{x}_0, t_0, \mathbf{v}(), \mathbf{a}(), \Psi)/dt$ ,  $t = t_0, \dots, t_0 + 10$  (with decay). (Scales differ between panels: note max and sum values.)

```
par(mfrow=c(3,4))
par(mar=0.1*c(1,1,1,1))
n0 <- 1
th <- 5
tm <- 7
for(t in 0:10) {
  amat <- outer(xvec,yvec, denratefunc, t=t,
                x0=x0,y0=y0,t0=0, vx=vx,vy=vy, ax=ax,ay=ay, teps=teps, n0=n0,th=th,tm=tm)
  #amat <- log(1+amat)
  #if(t==0) {
  #  amin <- min(amat)
  #  amax <- max(amat)
  #}
  amin <- min(amat)
  amax <- max(amat)
  breaks <- seq(from=amin, to=amax, length=length(colvec)+1)
  image(xvec, yvec, amat, asp=1, col=colvec, breaks=breaks, axes=FALSE)
  #image(xvec, yvec, amat,asp=1, main=bquote("Forwards with decay:" ~ t==.(t)), xlab="x", ylab="y",
  #      col=colvec, breaks=breaks)
  mtext(bquote("sum:" ~ .(sum(amat)) ~ "max:" ~ .(max(amat))), side=3, adj=1, cex=0.6, line=-1, col="white")
}
```



The total (equilibrium) mass density present is

$$\rho(\mathbf{x}, t | N_0, \mathbf{x}_0, \mathbf{v}(), \mathbf{a}(), \Psi) \quad (28)$$

$$= \rho(\mathbf{x} | N_0, \mathbf{x}_0, \mathbf{v}(), \mathbf{a}(), \Psi) \quad (29)$$

$$= \int_{-\infty}^t N_0 d(t - t_0 | T_h, T_m) p(\mathbf{x}, t | \mathbf{x}_0, t_0, \mathbf{v}(), \mathbf{a}(), \Psi) dt_0 \quad (30)$$

$$= N_0 \int_{t-T_m}^t e^{-\lambda(t-t_0)} g(\mathbf{x}, t - t_0 | \mathbf{x}_0, \mathbf{v}(), \mathbf{a}(), \Psi) dt_0 \quad (31)$$

$$= N_0 \int_0^{T_m} e^{-\lambda u} g(\mathbf{x}, u | \mathbf{x}_0, \mathbf{v}(), \mathbf{a}(), \Psi) du \quad (32)$$

$$= N_0 h(\mathbf{x} | \mathbf{x}_0, \mathbf{v}(), \mathbf{a}(), \Psi) \quad (33)$$

where

$$h(\mathbf{x} | \mathbf{x}_0, \mathbf{v}(), \mathbf{a}(), \Psi) = \int_0^{T_m} e^{-\lambda u} g(\mathbf{x}, u | \mathbf{x}_0, \mathbf{v}(), \mathbf{a}(), \Psi) du$$

The function  $h()$  retains the same symmetry as  $g()$ , so since

$$g(\mathbf{x}, u | \mathbf{x}_0, \mathbf{v}, \mathbf{a}, \Psi) = g(\mathbf{x}_0, u | \mathbf{x}, -\mathbf{v}, \mathbf{a}, \Psi)$$

it follows that

$$h(\mathbf{x}, u | \mathbf{x}_0, \mathbf{v}, \mathbf{a}, \Psi) = h(\mathbf{x}_0, u | \mathbf{x}, -\mathbf{v}, \mathbf{a}, \Psi)$$

In the Gaussian dispersal example

$$h(\mathbf{x} | \mathbf{x}_0, \mathbf{v}(), \mathbf{a}(), \Psi) = \frac{1}{2\pi\sqrt{a_x a_y}} \int_0^{T_m} \frac{e^{-\lambda u}}{u + t_\varepsilon} \exp\left(-\frac{(x - x_0 - v_x u)^2}{2a_x(u + t_\varepsilon)} - \frac{(y - y_0 - v_y u)^2}{2a_y(u + t_\varepsilon)}\right) du$$

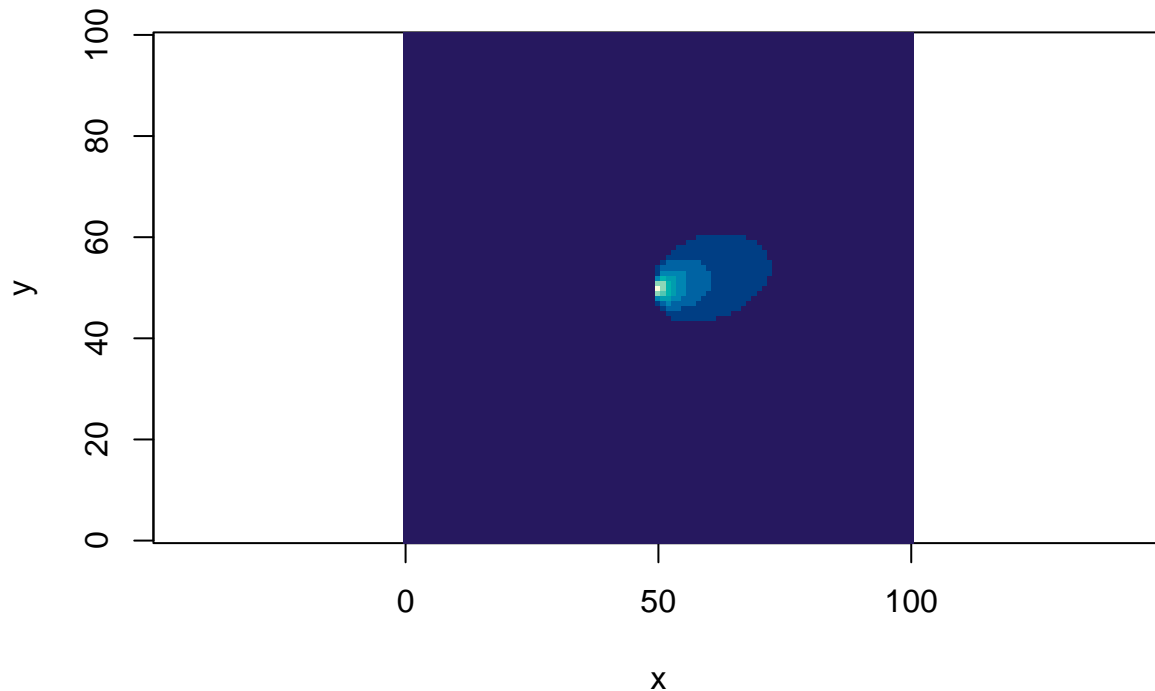


```
invisible()
#th <- 5
#tm <- 7
#ax <- 2^2; ay <- 5^2
#amat <- array(0,dim=c(nx,ny))
#nc <- 100
#for(i in 1:nc) {
#  t <- i/nc * 10
#  amat <- amat + outer(xvec,yvec, denratefunc, t=t,
#                        x0=x0,y0=y0,t0=0, vx=vx,vy=vy, ax=ax,ay=ay, teps=teps, n0=n0,th=th,tm=tm)
#}
#image(xvec, yvec, amat,asp=1,
#      main=bquote(t[h]==.(th) ~ ", " ~ t[m]==.(tm)),
#      xlab="x", ylab="y",col=colvec)
invisible()
```

Equilibrium Density:  $\rho(\mathbf{x}|N_0, \mathbf{x}_0, \mathbf{v}, \mathbf{a}, \Psi) = N_0 h(\mathbf{x}|\mathbf{x}_0, \mathbf{v}, \mathbf{a}, \Psi)$

```
th <- 5
tm <- 7
ax <- 2^2; ay <- 5^2
amat <- n0*outer(xvec,yvec, hfunc,
                 x0=x0,y0=y0, vx=vx,vy=vy, ax=ax,ay=ay, teps=teps, th=th,tm=tm)
image(xvec, yvec, amat, asp=1,
      main=bquote(h(x*"|"*x[0])*"." ~ x[0]==.(x0)*","*(y0)) ~ ", " ~ t[h]==.(th) ~ ", " ~ t[m]==.(tm)),
```

$h(\mathbf{x}|\mathbf{x}_0): \mathbf{x}_0 = (50,50) , t_h = 5 , t_m = 7$



The above figure plots, for a continuous fixed source of rate  $N_0$  at location  $\mathbf{x}_0$ , the equilibrium density at all locations  $\mathbf{x}$ :  $N_0 h(\mathbf{x}|\mathbf{x}_0)$ .

Now plot at each  $\mathbf{x}_0$  the equilibrium density at  $\mathbf{x}_1$  (in the centre of the diagram) that would result from a

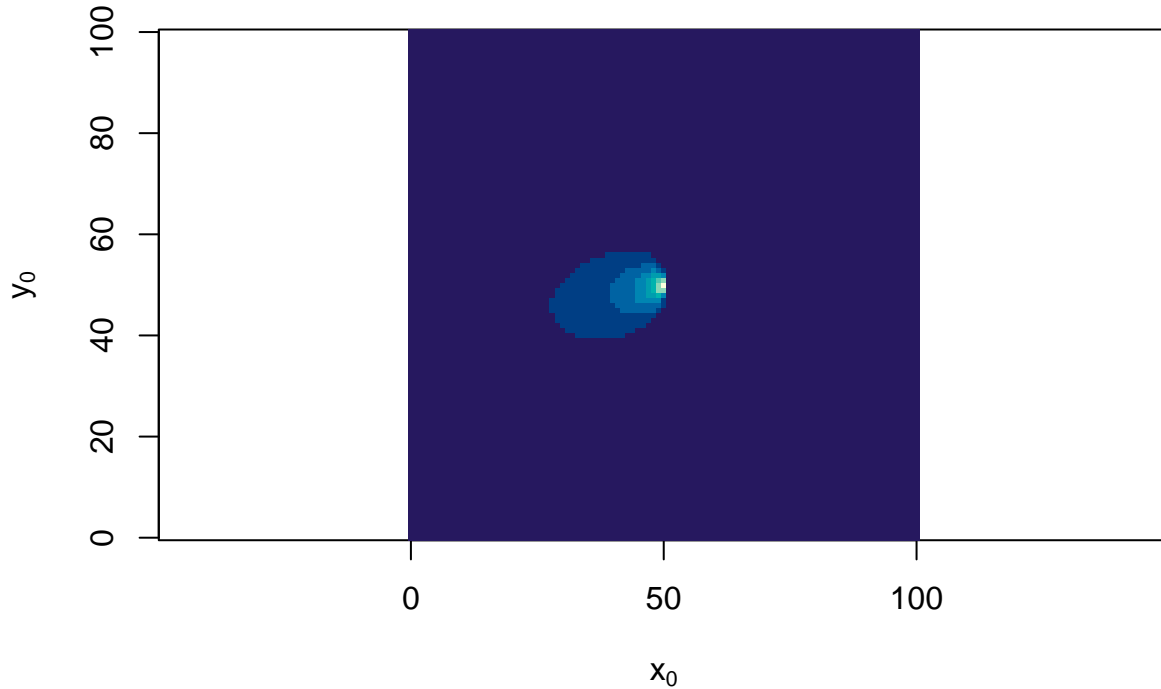
continuous source at  $\mathbf{x}_0$ . i.e.  $N_0 h(\mathbf{x}_1 | \mathbf{x}_0)$

$$\begin{aligned} N_0 \tilde{h}(\mathbf{x}_0 | \mathbf{x}_1, \mathbf{v}, \mathbf{a}, \Psi) &= N_0 h(\mathbf{x}_1 | \mathbf{x}_0, \mathbf{v}, \mathbf{a}, \Psi) \\ &= N_0 h(\mathbf{x}_0 | \mathbf{x}_1, -\mathbf{v}, \mathbf{a}, \Psi) \end{aligned}$$

$$N_0 \tilde{h}(\mathbf{x}_0 | \mathbf{x}_1, \mathbf{v}, \mathbf{a}, \Psi) = N_0 h(\mathbf{x}_1 | \mathbf{x}_0, \mathbf{v}, \mathbf{a}, \Psi) = N_0 h(\mathbf{x}_0 | \mathbf{x}_1, -\mathbf{v}, \mathbf{a}, \Psi)$$

```
th <- 5
tm <- 7
ax <- 2^2; ay <- 5^2
x1 <- 50; y1 <- 50
rho1 <- 1; mu <- 1
amat <- outer(xvec,yvec, function(x0vec,y0vec) {
  apply(cbind(x0vec,y0vec),1,function(x0y0) {
    hfunc(x=x1,y=y1,x0=x0y0[1],y0=x0y0[2],
          vx=vx,vy=vy, ax=ax,ay=ay, teps=teps, th=th,tm=tm)
  })
})
dim(amat) <- c(length(xvec),length(yvec))
image(xvec, yvec, amat, asp=1,
      main=bquote(h(x[1]*"|"*x[0])*":" ~ x[1]==.(x0)*","*(y0)) ~ "," ~ t[h]==.(th) ~ "," ~ t[m]==.(tm)),
      xlab=expression(x[0]), ylab=expression(y[0]), col=colvec)
```

$h(\mathbf{x}_1 | \mathbf{x}_0)$ :  $\mathbf{x}_1 = (50, 50)$ ,  $t_h = 5$ ,  $t_m = 7$



(Computing this the other way using the symmetry of  $h()$ )

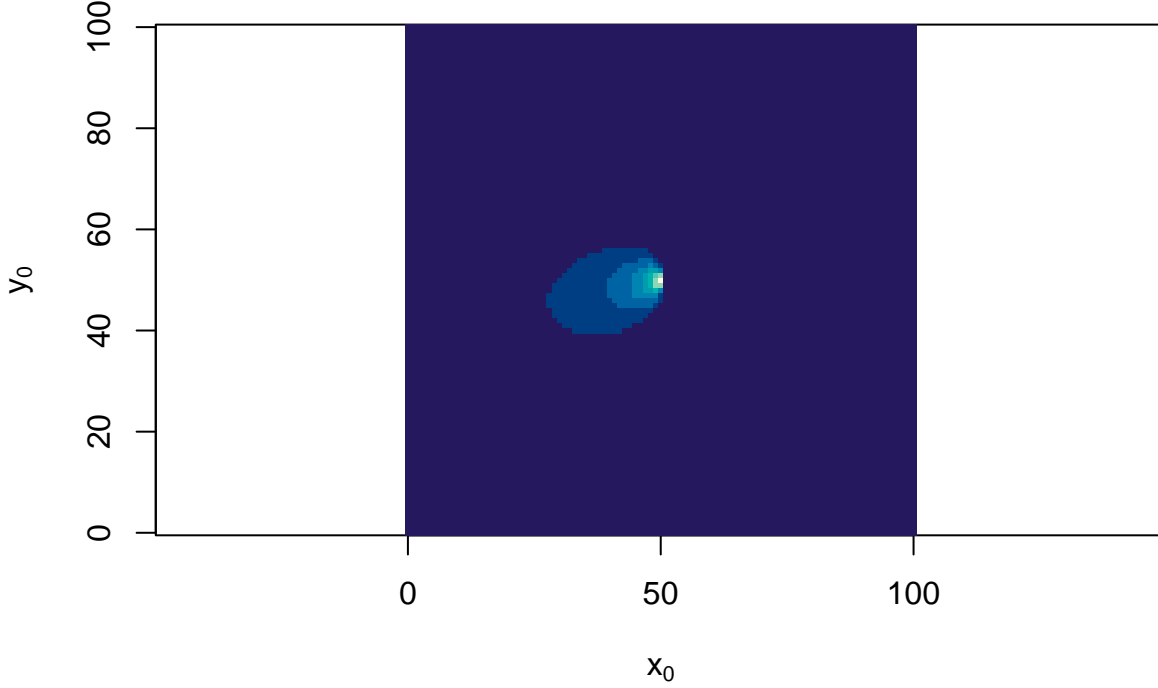
```
th <- 5
tm <- 7
ax <- 2^2; ay <- 5^2
x1 <- 50; y1 <- 50
rho1 <- 1; mu <- 1
amat <- n0*outer(xvec,yvec, hfunc,
```

```

x0=x1,y0=y1, vx=-vx,vy=-vy, ax=ax,ay=ay, teps=teps, th=th,tm=tm)
image(xvec, yvec, amat, asp=1,
      main=bquote(h(x[1]*"|"*x[0])*": " ~ x[1]==(. (x0)*", "*.(y0)) ~ ", " ~ t[h]==.(th) ~ ", " ~ t[m]==.(tm)
      xlab=expression(x[0]), ylab=expression(y[0]), col=colvec)

```

$h(\mathbf{x}_1|\mathbf{x}_0): \mathbf{x}_1 = (50,50), t_h = 5, t_m = 7$



## Probabilistic Inversion

Now assume that at some location  $\mathbf{x}_1$  we observe a density  $\rho_1$ , and that this is an observation made with error:

$$\rho_1 | \rho_1^*, \sigma_e \sim N(\rho_1^*, \sigma_e^2)$$

where the true density is  $\rho_1^*$  and the error variance is  $\sigma_e^2$ .

Assume that there is a single continuous source of unknown strength  $N_0$  and unknown location  $\mathbf{x}_0$ . Priors for the strength and location are  $\pi(N_0)$  and  $\pi(\mathbf{x}_0)$  respectively.

Assume that the velocity field  $\mathbf{v}()$  and the diffusion field  $\mathbf{a}()$  are known.

Using the results from the previous section, conditional on  $N_0$  and  $\mathbf{x}_0$  the observed density at  $\mathbf{x}_1$  is

$$\rho_1^* = N_0 h(\mathbf{x}_1 | \mathbf{x}_0, \mathbf{v}(), \mathbf{a}(), \Psi)$$

which we write for brevity as

$$\rho_1^* = h_1^*(\mathbf{x}_0) = h_1^*$$

but noting its dependence on  $\mathbf{x}_0$ .

It follows that the joint distribution of the unknown source strength  $N_0$  and location  $\mathbf{x}_0$  is

$$\begin{aligned}
p(N_0, \mathbf{x}_0 | \rho_1, \mathbf{x}_1) &\propto \pi(N_0) \pi(\mathbf{x}_0) \exp \left( -\frac{1}{2\sigma_e^2} [\rho_1 - N_0 h_1^*(\mathbf{x}_0)]^2 \right) \\
&\propto \pi(N_0) \pi(\mathbf{x}_0) \exp \left( -\frac{(h_1^*)^2}{2\sigma_e^2} \left[ N_0 - \frac{\rho_1}{h_1^*} \right]^2 \right)
\end{aligned}$$

A suitable prior for  $N_0$  is the Exponential( $\mu$ ) distribution

$$\begin{aligned} N_0 &\sim \text{Exp}(\mu) \\ \pi(N_0) &= \mu e^{-\mu N_0} \end{aligned}$$

This can be marginalised out of the posterior distribution as follows. Firstly the joint distribution is

$$\begin{aligned} p(N_0, \mathbf{x}_0 | \rho_1, \mathbf{x}_1) &\propto \pi(\mathbf{x}_0) e^{-\mu N_0} \exp\left(-\frac{(h_1^*)^2}{2\sigma_e^2} \left[N_0 - \frac{\rho_1}{h_1^*}\right]^2\right) \\ &\propto \pi(\mathbf{x}_0) \exp\left(-\frac{(h_1^*)^2}{2\sigma_e^2} \left[N_0 - \left(\frac{\rho_1}{h_1^*} - \frac{\mu\sigma_e^2}{(h_1^*)^2}\right)\right]^2 - \frac{\rho_1\mu}{h_1^*} + \frac{\mu^2\sigma_e^2}{2(h_1^*)^2}\right) \end{aligned}$$

Integrating out  $N_0$  leads to

$$p(\mathbf{x}_0 | \rho_1, \mathbf{x}_1) \propto \pi(\mathbf{x}_0) \frac{\sigma_e}{h_1^*} \exp\left(-\frac{\rho_1\mu}{h_1^*} + \frac{\mu^2\sigma_e^2}{2(h_1^*)^2}\right)$$

If we let  $\sigma_e \rightarrow 0$  (indicating very accurate observations) we are left with a very simple form for the posterior:

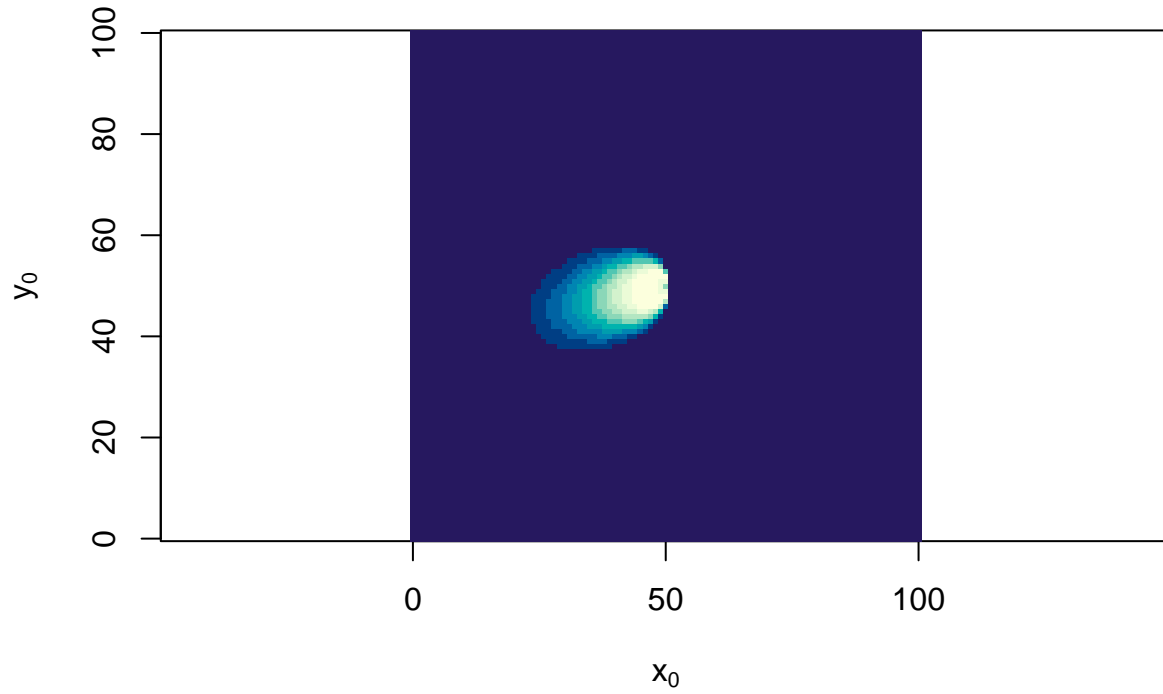
$$p(\mathbf{x}_0 | \rho_1, \mathbf{x}_1) \propto \pi(\mathbf{x}_0) \frac{1}{h_1^*} e^{\frac{\rho_1\mu}{h_1^*}}$$

which we plot below for a uniform prior on the source location  $\pi(\mathbf{x}_0) \propto 1$ .

```
th <- 5
tm <- 7
ax <- 2^2; ay <- 5^2
x1 <- 50; y1 <- 50
rho1 <- 1; mu <- 1
amat <- n0*outer(xvec,yvec, hfunc,
                 x0=x1,y0=y1, vx=-vx,vy=-vy, ax=ax,ay=ay, teps=teps, th=th,tm=tm)

qmat <- exp(-max(amat)/3.0/amat) * (1/amat)
image(xvec, yvec, qmat, asp=1,
      main=bquote(p(x[0]*"|"*x[1])*":" ~ x[1]==(. (x0)*", "*.(y0)) ~ ", " ~ t[h]==.(th) ~ ", " ~ t[m]==.(tm)
      xlab=expression(x[0]), ylab=expression(y[0]), col=colvec)
```

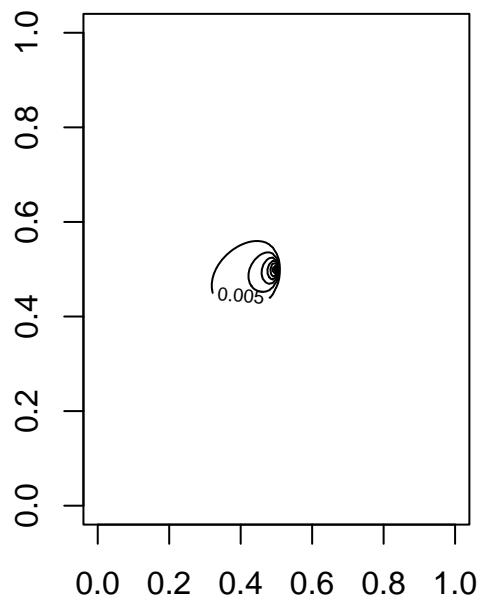
$p(x_0|x_1): x_1 = (50,50) , t_h = 5 , t_m = 7$



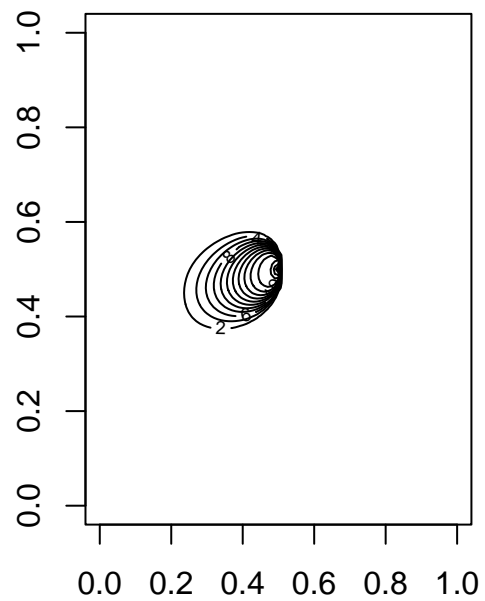
Plotting again, but as a contour map

```
par(mfrow=c(1,2))
contour(amat, main=expression(h(x[0]*"|"*x[1])))
contour(qmat, main=expression(p(x[0]*"|"*x[1])))
```

$h(x_0|x_1)$



$p(x_0|x_1)$

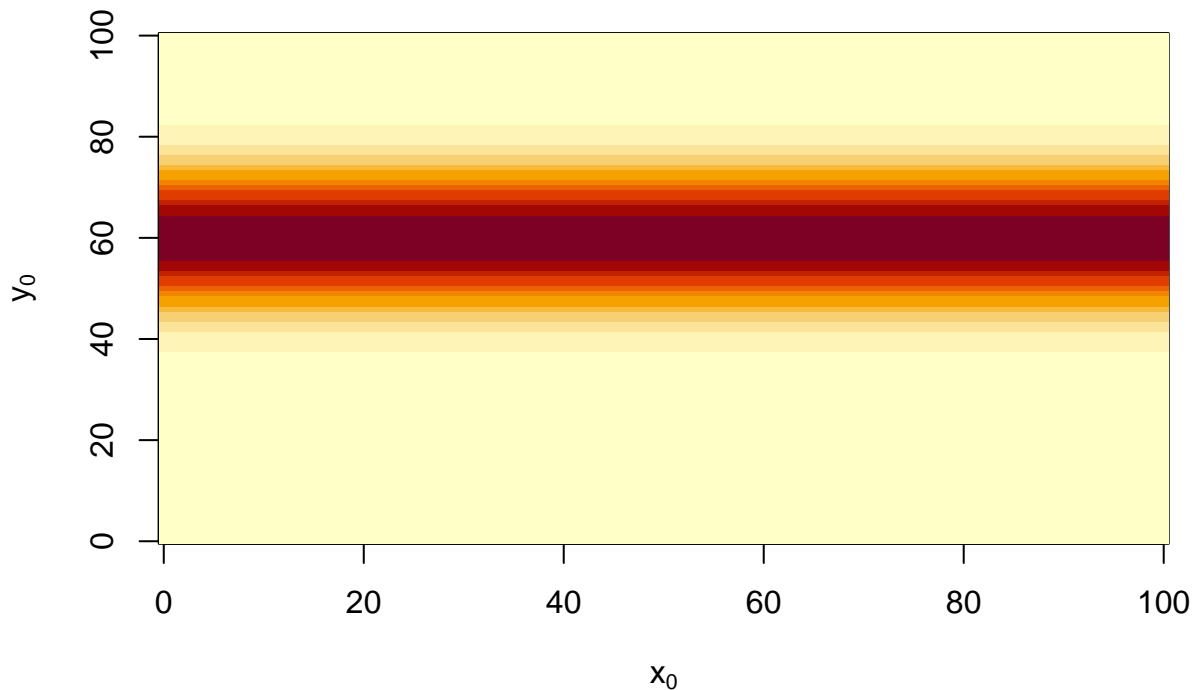


A different prior: e.g. normally distributed in  $y$  (centered on  $y_a$  with standard deviation  $\sigma_a$ ) and uniform in  $x$ :

$$\pi(\mathbf{x}_0) \propto \exp\left(-\frac{1}{2\sigma_a^2} [x_{0y} - y_a]^2\right)$$

```
ya <- 60
sigmaa <- 10
p0mat <- t(array(exp(-0.5*(yvec-ya)^2/sigmaa^2), dim=dim(amat)))
image(xvec, yvec, p0mat, main=bquote(pi(x[0]) %prop% N[y](.(ya),.(sigmaa)^2)),
      xlab=expression(x[0]), ylab=expression(y[0]))
```

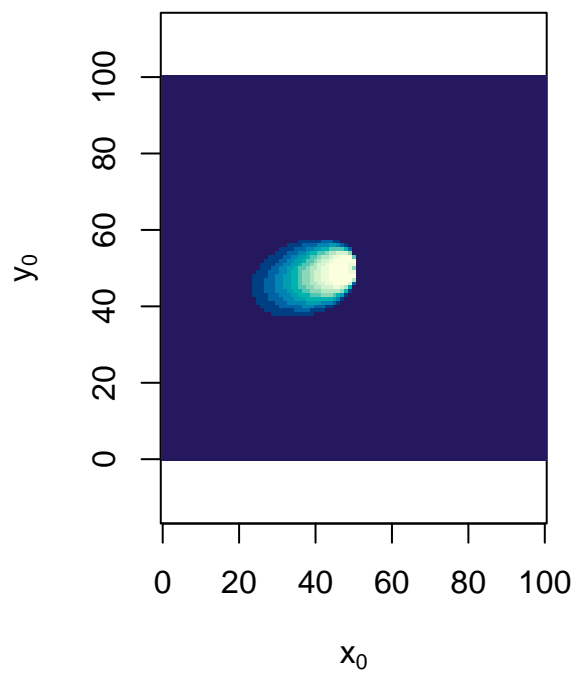
$$\pi(\mathbf{x}_0) \propto N_y(60, 10^2)$$



The effect of the prior is shown at right below

```
par(mfrow=c(1,2))
image(xvec, yvec, qmat, asp=1,
      main=bquote(p(x[0]*"|"*x[1])*":" ~ pi(x[0]) %prop% 1),
      xlab=expression(x[0]), ylab=expression(y[0]), col=colvec)
image(xvec, yvec, p0mat*qmat, asp=1,
      main=bquote(p(x[0]*"|"*x[1])*":" ~ pi(x[0]) %prop% N[y](.(ya),.(sigmaa)^2)),
      xlab=expression(x[0]), ylab=expression(y[0]), col=colvec)
```

$$p(x_0|x_1): \pi(x_0) \propto 1$$



$$p(x_0|x_1): \pi(x_0) \propto N_y(60, 10^2)$$

